VOL. V, NO. 3 SEPTEMBER, 1930

THE QUARTERLY REVIEW
of BIOLOGY

THE FOOT MUSCULATURE OF THE HIGHLAND GORILLA (GORILLA BERINGEI)

BY WILLIAM L. STRAUS, JR.
Department of Anatomy, Johns Hopkins University

THE musculature of the gorilla foot is fairly well known. It has received the attention of a number of investigators. Some of these workers have, however, confined their attentions to specific muscles, while others have described in detail only those muscles which differed markedly from the usual condition in man. Most striking perhaps is the lack of adequate illustrations (except in the beautifully illustrated monograph of Duvernoy). In connection with studies on Primate feet, I recently was able, through the courtesy of Dr. William K. Gregory of the American Museum of Natural History, to dissect the right foot of an adult female highland gorilla, of the species *Gorilla beringei* (Amer. Mus. Nat. Hist., Compar. Anat. No. 47). This foot was obtained in East Africa by the late Carl Akeley.

I believe that I am correct in affirming this to be the first description of the complete foot musculature of the highland gorilla of East Africa. Morton (1924) studied the left foot of the animal described herein, but his account is confined to a description of the *M. peroneus tertius*. My assumption is based upon the date of discovery of *Gorilla beringei*. This highland form of gorilla was first made known in 1901 by von Beringe, hence its name (Derscheid, 1927). There is therefore no doubt that the specimens of gorilla described prior to this data are of the lowland type, *Gorilla gorilla*. My search of the literature has yielded four accounts since 1901 which consider the muscles of the gorilla foot. The gorilla dissected by Sommer (1906) is without doubt of the species *G. gorilla* (see Schultz, 1927). That studied by Pira (1913–14) was from the French Congo, and was almost certainly *G. gorilla*, since *G. beringei* is not known to occur in that area. The infantile gorillas of the Zürich collection in which Loth (1908) described the *aponeurosis plantaris* and Sawalischin (1911) the *M. flexor digitorum brevis*, are definitely stated by these authors to be specimens of *G. gorilla*.

Although the highland gorilla has been denied the rank of a separate species by some authors (e.g., Derscheid and Coolidge, both of whom regard it as merely a subspecies of *Gorilla gorilla*, and designate it *Gorilla gorilla beringei*), there is evidence which indicates that it differs considerably

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

from the West African or lowland gorilla (*Gorilla gorilla*), particularly in the outer form of the foot and hand, and in the proportions of the limb bones (Schultz, 1927). The foot of the highland gorilla seems to be relatively broader than that of the lowland form; the heel is broader and better developed; the great toe is relatively longer, and the free digital length much less. This naturally leads us to the question: Does the highland gorilla differ from the lowland gorilla in the structure and arrangement of the muscles of the foot, and if so, to what degree? I shall attempt to throw light upon this question, in so far as the very limited amount of material permits.

The literature dealing with the foot muscles of *Gorilla gorilla* has been indispensable in this study, because it has made it possible for me to compare that species with *G. beringei* and to consider the known range of variation. I have not, however, attempted to consider fully the papers dealing with other Primates. In addition to the foot of the *G. beringei* upon which this study is based, I have had the opportunity of making certain observations upon an infant female *G. gorilla* (Amer. Mus. Nat. Hist., Comp. Anat. №1105) dissected by Dr. Dudley J. Morton. Furthermore, I have studied the pedal interosseous muscles of a juvenile female *G. beringei* (Coll. of Labor. of Phys. Anthrop., Johns Hopkins University, № 7) and an infant female *G. gorilla* (Coll. of Labor. of Phys. Anthrop., Johns Hopkins University, №5). Specimens of additional Primates dissected by me in connection with other work will also be referred to from time to time.

These specimens are as follows: left foot of a juvenile male chimpanzee (*Pan chimpanse*), №162; left foot of a juvenile male orang-utan (*Pongo pygmaeus*), №37; left foot of an adult female gray gibbon (*Hylobates pileatus*), №133; right foot of an adult langur (*Pygathrix germaini*), №134; and left foot of an adult galago (*Galago* (sp.?)), №221436. The first four specimens are from the collection of the Department of Anatomy, Johns Hopkins University. The chimpanzee and orang feet (№162 and №37) are from animals which are being dissected in this laboratory by Mr. T. D. Stewart. The galago is from the Division of Mammals, U. S. National Museum.

I wish to thank Dr. W. K. Gregory for the unique opportunity of studying the foot of the adult *G. beringei*, and for allowing me to examine the dissection of the young *G. gorilla* made by Dr. D. J. Morton. I also wish to thank Dr. Morton, who very obligingly permitted me to study his dissection. In addition thanks are due Mr. Gerrit S. Miller, Jr., for the opportunity of dissecting the specimen of *Galago*.

I have considered it necessary in this study to ascertain the innervation of the muscles, whenever possible, because of the clues given thereby to the identification of certain muscles and their elements. This is particularly important in a consideration of the deep plantar musculature, where it sometimes becomes necessary, as in the specimen of *G. beringei* under consideration, to decide whether the outer (fibular) head of the *M. flexor hallucis brevis* is completely absent or whether it has become incorporated in the *M. adductor hallucis*. Such a question can be decided only by recourse to the innervation. Homology based upon innervation necessarily is a consequence of the acceptance of the hypothesis of Fürbringer (1888), which assumes a constant relationship between peripheral nerve and striated muscle throughout development. An excellent exposition of this hypothesis, with examples from the facialis musculature, has been given by Huber (1925).

In a relatively simple nerve such as the facial, the nerve-muscle relation, as Huber has shown, seems well-established. But when dealing with the limb-plexuses, the theory apparently is open to exceptions. Such apparent exceptions have been dealt with, for example, by Cunningham (1882). The limb-plexuses are of such complex structure that it is next to impossible to decide whether the exceptions to the Fürbringer hypothesis are real or apparent. Confining myself merely to the foot, I desire to discuss a few muscles that exhibit inconstant nerve-supply, as every anatomist knows. The *lumbricales*, particu-

larly those for the third and fourth toes, may at times be innervated by the medial plantar nerve, at times by the lateral, and occasionally by both. This may be explained by discarding the Fürbringer hypothesis and by considering that the muscle areas supplied by the plantar nerves are not sharply defined, or by assuming the possibility of a heterotopic or secondary innervation. On the other hand, an explanation may be offered on the basis of the nerve-muscle hypothesis. It is of course possible that in such a complicated arrangement as a limb-plexus, nerve-fibres may not always follow their accustomed paths. Therefore, fibres nominally belonging to one plantar nerve may sometimes be carried with those of the other plantar nerve. Muscles may therefore receive an innervation that is macroscopically anomalous, or the innervation may seem to vary, whereas it actually does not. Again, wherever the muscle fields supplied by two nerves lie so close together, as in the case of the plantar nerves, there is always the strong possibility, even probability, that certain muscles on or near the boundary line may at times be derived from the muscle anlagen supplied by one nerve, at times from the muscle anlagen of the other nerve. This last reasoning could apply not only to the *lumbricales*, but also to the *M. flexor digitorum brevis pedis*. This muscle is usually innervated by the medial plantar nerve alone. Not infrequently, however, in addition to its usual nerve, a twig from the lateral plantar nerve may enter the outer border of the muscle, supplying the portion of the belly which gives rise to the tendon for the fifth toe. There is no need to regard this as due to secondary innervation; it may be explained by assuming that the lateral portion of the muscle may at times be derived from the field of the lateral plantar nerve. Similar explanations, on the basis of the Fürbringer hypothesis, can be given for the occasional branch from the lateral plantar nerve to the fibular head of the *M. flexor hallucis brevis*, or the occasional medial plantar twig to the oblique head of the *M. adductor hallucis*, both of which conditions may occur in otherwise normal feet. At the lateral margin of the great toe the fields of the two plantar nerves lie close together. It is therefore not difficult to believe that the flexor sometimes contains muscle-fibres from the lateral plantar anlagen, and the adductor occasionally from the medial plantar anlagen. These two muscles, in particular, may exhibit varying degrees of fusion (orang-utan of Ruge (1878b), gorilla of Straus), a further indication of the instability of this muscle area. Without necessarily assuming that the Fürbringer hypothesis is an established fact, and despite its very definite limitations, especially when working with the nerves of the limb-plexuses, this idea is nevertheless the best guide in homologizing muscles at the present time. It is of tremendous value in phylogenetic investigations. I have therefore applied this principle of nerve-muscle relationship in my work, although I fully realize that it must always be used with reservation, especially in the extremities.

DESCRIPTION OF MUSCLES OF FOOT OF THE ADULT FEMALE (№ 47) GORILLA BERINGEI

The foot was skinned in the field by Mr. Akeley, and it was removed from the leg at the ankle joint. I was therefore unable to study the origins and innervations of the muscles which arise outside of the foot itself, nor am I able to discuss the cutaneous innervation. A brief preliminary report of the foot musculature of this specimen has already been published (see Straus, 1929a).

Muscles of the Sole

Aponeurosis plantaris (fig. 1). This arises from the *tuber calcanei* and extends forward over the middle of the foot to the region about the heads of the metatarsals. Although the part of the aponeurosis over the body and base of the second and the body of the third metatarsals had, unfortunately, been removed in the skinning, the essential details could be made out.

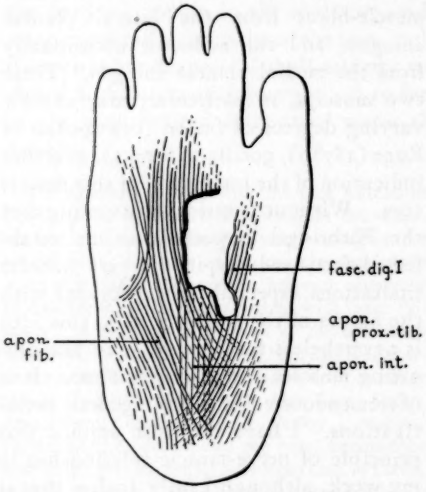


FIG. 1. GORILLA BERINGEI (No. 47). PLANTAR APONEUROSIS

apon. fib. = aponeurosis fibularis; *apon. int.* = aponeurosis intermedialis; *apon. prox.-tib.* = aponeurosis proximo-tibialis; *fasc. dig. I* = fasciculus digiti I. × approx. $\frac{8}{10}$ natural size.

There is a definite *aponeurosis intermedialis*, crossed at about the middle of the sole by the *aponeurosis tibialis proximo-medialis*, which in turn is crossed above by the *fasciculus digiti I*. The outer portion of the *aponeurosis fibularis* stops at about the end of the tarsus, over the *abductor digiti V*, where it thins out, the remainder running toward the digital region; it has a strong attachment to the base of the fifth metatarsal. The *fasciculus digiti I* thins out over the proximal part of the belly of the *abductor hallucis*. There are strong, deep processes from the fibular side of the aponeurosis. All of the various elements of the aponeurosis mingle in the region of the heel. The greatest thickness is over heel and tarsus (about 3 mm. over the former).

M. abductor hallucis (figs. 2, 4, 9, 10). This is a large and powerful muscle, arising from the medial process of the *tuber calcanei*, the laciniate ligament and under surface of the plantar aponeurosis. The lateral fibres of origin mingle with those of the *flexor digitorum brevis*. The powerful muscle-belly is prolonged as a flat tendon, to which are joined, on each side, the fibres of the tibial (inner) head of the *flexor hallucis brevis*, and which is inserted into the medial side of the base of the basal phalanx of the hallux and the metatarsophalangeal joint capsule of that toe. *Innervation:* by a branch from the main trunk of the medial plantar nerve.

M. abductor digiti V (figs. 2, 3, 4). This is a well-developed muscle, arising chiefly from the plantar and lateral surfaces of the *tuber calcanei*, as far lateral as the *processus peroneus* (see Weidenreich, 1922), with an additional origin from the under surface of the plantar aponeurosis. The most medial fibres of origin touch those of the superficial head of the *flexor digitorum brevis*. The more lateral fibres, arising from the *processus peroneus* and lateral surface of the calcaneus, split off from the main mass of muscle not far beyond their origin and insert fleshily into the tuberosity of the fifth metatarsal bone, forming a *M. abductor ossis metatarsi V* (figs. 2, 3). The rest of the muscle is prolonged into a tendon which pierces the muscle mass of the *flexor digiti V brevis*, lying between the superficial and deep layers of the latter, and inserts into the fibular side of the base of the basal phalanx of the fifth toe.

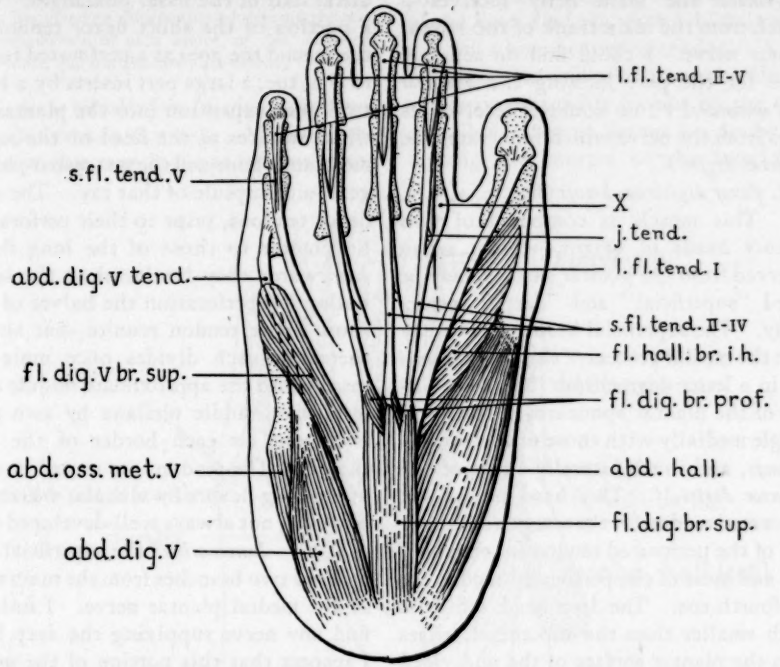


FIG. 2. GORILLA BERINGEI (No. 47). SUPERFICIAL PLANTAR MUSCLES

abd. dig. V = abductor digiti V; *abd. hall.* = abductor hallucis; *abd. oss. met. V* = abductor ossis metatarsi V; *fl. dig. br. prof.* = deep head of flexor digitorum brevis; *fl. dig. br. sup.* = superficial head of flexor digitorum brevis; *fl. dig. V br. sup.* = superficial layer of flexor digiti V brevis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *j. tend.* = vincula; *l. fl. tend.* = long flexor tendon; *s. fl. tend.* = short flexor tendon; X = tendinous slip from short flexor tendon II to second metatarso-phalangeal joint. × approx. $\frac{2}{3}$ natural size.

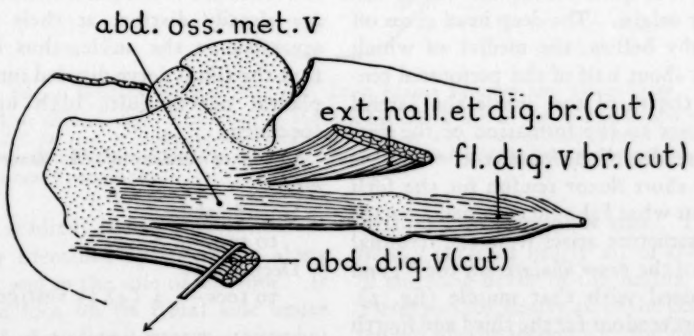


FIG. 3. GORILLA BERINGEI (No. 47). LATERAL VIEW OF FOOT

abd. dig. V = abductor digiti V; *abd. oss. met. V* = abductor ossis metatarsi V; *ext. hall. et dig. br.* = short extensors; *fl. dig. V br.* = flexor digiti V brevis. × approx. $\frac{1}{2}$ natural size.

Innervation: the main belly receives a branch from the main trunk of the lateral plantar nerve. I could find no separate nerve for the part forming the *abductor ossis metatarsi V;* no doubt it receives its fibres from the nerve which innervates the *abductor digiti V.*

M. flexor digitorum brevis (figs. 2, 4, 5, 7, 15). This muscle is composed of two distinct heads of origin, which, when observed from the plantar surface, may be called "superficial" and "deep," respectively. The superficial head arises chiefly from the medial process of the *tuber calcanei* and in a lesser degree from the under surface of the plantar aponeurosis; the fibres mingle medially with those of the *abductor hallucis,* and touch laterally those of the *abductor digiti V.* This head provides a perforated tendon for the second toe, about half of the perforated tendon for the third toe, and most of the perforated tendon for the fourth toe. The deep head, which is much smaller than the superficial, arises from the plantar surface of the undivided tendon of the *flexor tibialis* before the latter joins the tendon of the *flexor fibularis.* This head is fleshy on its plantar aspect. It must have extended up into the leg, for at the ankle, where the muscle has been severed, it is quite robust and clearly has a higher origin. The deep head gives off two fleshy bellies, the medial of which supplies about half of the perforated tendon of the third toe, while the lateral contributes to the formation of the perforated tendon of the fourth toe. There is no true short flexor tendon for the fifth digit, but what I should consider a vestige of this structure arises from the terminal tendon of the *flexor fibularis* for toe V, and is discussed with that muscle (fig. 2). The short tendons for the third and fourth toes are perforated, as in man, by the long flexor tendons of those digits, this perforation occurring at about the middle or distal half of the basal phalanges. Only a portion of the short flexor tendon for the second toe goes as a perforated tendon to that toe; a large part inserts by a broad tendinous expansion into the plantar and tibial surfaces of the head of the second metatarsal bone and the metatarso-phalangeal joint-capsule of that ray. The short flexor tendons, prior to their perforation, lie plantar to those of the long flexor. Afterwards they lie dorsal to the latter. Following perforation the halves of each short flexor tendon reunite, but shortly thereafter each divides once more and inserts into the approximate middle of its respective middle phalanx by two processes, one on each border of the bone (fig. 7). The tendons are united to those of the long flexors by vincula, which are, however, not always well-developed (figs. 2, 4, 7). *Innervation:* the superficial head receives two branches from the main trunk of the medial plantar nerve. I failed to find any nerve supplying the deep head. I suspect that this portion of the muscle receives its nerve above the ankle, for the muscle fibres, as I have previously mentioned, show definite signs of having a higher extension. Such a nerve may have come directly from the tibial nerve, or else from one of the plantar nerves, which are already distinct at their points of severance in the ankle, thus indicating that the tibial nerve divided into the two plantar nerves quite high up in this specimen.

Origin of tendons of M. flexor digitorum brevis

Superficial head:
to toes—2 3 4
Deep head
to toes— 3 (4) (5 vestige)

(In this and similar tables, where an end tendon receives contributions from two sources, that part of the tendon which supplies the minor portion is enclosed by parentheses. When there are two sources,

and neither figure is enclosed by parentheses, the author has given no information concerning the relative contribution of each source, or else, as in the above table, the contributions are equal.)

M. flexor tibialis (= *M. flexor digitorum longus*) (figs. 2, 4, 6, 7, 15). Although the origin of this muscle is not present in the specimen studied, it can nevertheless be accurately identified by its course along the ankle and in the sole of the foot. It enters the foot on its tibial side under cover of the laciniate ligament, its tendon lying just posterior to that of the *tibialis posterior*. In the sole the tendon of the tibial flexor lies slightly superficial to that of the *flexor fibularis*, with which it unites to form a broad common tendon. A careful dissection and tracing of the fibres in the common tendon formed by the tibial and fibular flexors leaves no doubt concerning the sources of the long flexor tendons of the various toes. The *flexor tibialis* supplies nearly all of the tendon of the long flexor of the hallux from its dorsal surface, nearly all of the perforating tendon for the second toe, the minor portion of the perforating tendon of the third toe, and only a small portion of the per-

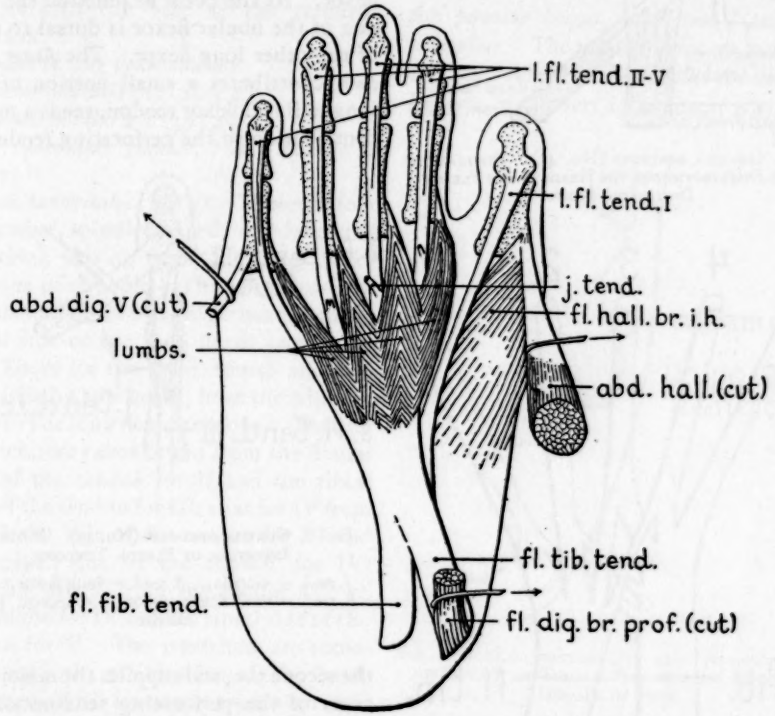


FIG. 4. GORILLA BERINGEI (No. 47). LONG FLEXOR TENDONS AND LUMBRICALES

abd. dig. V = abductor digiti V; *abd. hall.* = abductor hallucis; *fl. dig. br. prof.* = deep head of flexor digitorum brevis; *fl. fib. tend.* = tendon of flexor fibularis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *fl. tib. tendon* = tendon of flexor tibialis; *j. tend.* = vincula; *l. fl. tend.* = long flexor tendon; *lumbs.* = lumbricales. × approx. $\frac{2}{3}$ natural size.

forating tendon of the fourth toe. As I have already stated, the deep head of the *flexor digitorum brevis* arises from the plantar surface of the long tibial flexor.

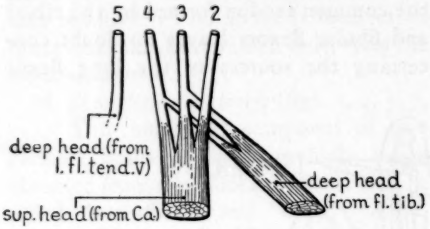


FIG. 5. GORILLA BERINGEI (No. 47). DIAGRAM TO SHOW DISTRIBUTION OF THE HEADS OF THE FLEXOR DIGITORUM BREVIS

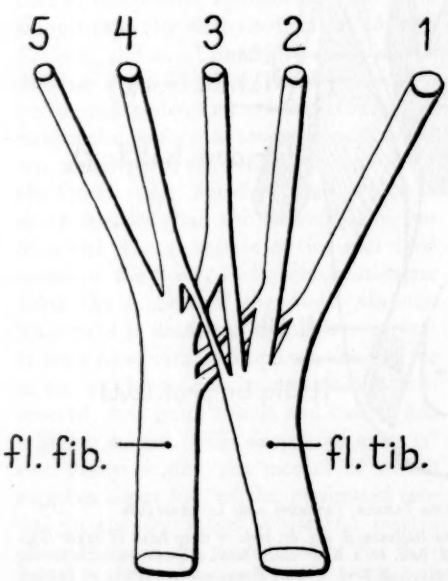


FIG. 6. GORILLA BERINGEI (No. 47). DIAGRAM TO SHOW DISTRIBUTION OF THE LONG FLEXOR TENDONS

fl. fib. = flexor fibularis; *fl. tib.* = flexor tibialis

M. flexor fibularis (= *M. flexor hallucis longus*) (figs. 2, 4, 6, 7, 15). Like that of the flexor tibialis, the origin of this muscle is lacking. Its identity can likewise be established by its position in ankle and foot. The rounded tendon goes along the *sulcus M. flexoris hallucis longi* of the talus and calcaneus, under cover of the laciniate ligament, posterior to the tendon of the *flexor tibialis*, over the plantar surface of the *sustentaculum tali*, and along the sole of the foot to join the tendon of the tibial flexor. At the point of junction the tendon of the fibular flexor is dorsal to that of the other long flexor. The *flexor fibularis* contributes a small portion of the long hallucal flexor tendon, sends a minor contribution to the perforating tendon of

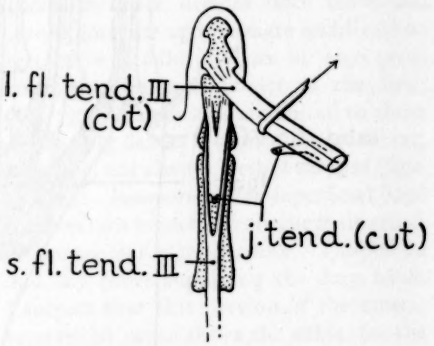


FIG. 7. GORILLA BERINGEI (No. 47). MODE OF INSERTION OF FLEXOR TENDONS

j. tend. = vincula; *l. fl. tend.* = long flexor tendon; *s. fl. tend.* = short flexor tendon. × approx. ½ natural size.

the second toe, and supplies the major portions of the perforating tendons of the third and fourth toes, and all of the long flexor tendon of the fifth toe. The long flexor tendons for the four lateral toes (after perforating the short flexor tendons of their respective digits) are inserted into the bases of the terminal phalanges. There is no perforated (short flexor) tendon for the fifth toe, but the terminal long flexor tendon for that digit gives off, from its dorsal aspect, a very definite tendon which inserts into the middle phalanx of toe V as do the perforated tendons of the

other toes. This accessory tendon seems undoubtedly to represent the short flexor tendon of V which has become attached to the long flexor tendon of that toe. The course of the long flexor tendon of the great toe lies, as in man, between the heads of the *flexor hallucis brevis* and it inserts into the base of the terminal phalanx.

Source of long flexor tendons:

Flexor fibularis (1) (2) 3 4 5.

Flexor tibialis 1 2 (3) (4).

M. quadratus plantae. This muscle is absent.

Mm. lumbricales (fig. 4). These are four in number, spindle-shaped, very large and powerful, arising from the long flexor tendons in the sole. The innermost (for second toe) arises by a single head from the tibial side of the long flexor tendon for II. Those for the third, fourth and fifth toes arise by two heads, from the adjacent sides of the long flexor tendons. That for III therefore takes origin from the fibular side of the tendon for II and the tibial side of the tendon for III; that for IV from the fibular side of the tendon for III and the tibial side of the tendon for IV; and that for V from the fibular side of the tendon for IV and the tibial side of the tendon for V. The insertions are somewhat into the tibial sides of the basal phalanges of the four outer toes, with very definite extensions (narrow tendons) into the extensor aponeuroses. *Innervation:* the *lumbricales* for toes II, III and IV receive branches from the medial plantar nerve, that for toe V from the superficial ramus of the lateral plantar nerve.

M. tibialis posterior (figs. 8, 15). The tendon lies anterior to that of the *flexor tibialis*, and posterior to those of the *tibialis anterior*. It passes under cover of the laciniate ligament and inserts by a broad, flat tendon on the medial and plantar surfaces of the tuberosity of the *navicular*e, is prolonged to the plantar surfaces of the cuneiforms, and also sends fibres to the *sustentaculum tali* and sheath of the *peroneus longus*.

M. flexor hallucis brevis (figs. 2, 4, 9, 10). This is a large and well-developed muscle. The tibial head arises from the sheath of the *peroneus longus*, *cuneiforme I* and the *naviculare*. The muscle-fibres are attached on either side of the tendon of the *abductor hallucis*, and insert in common with this

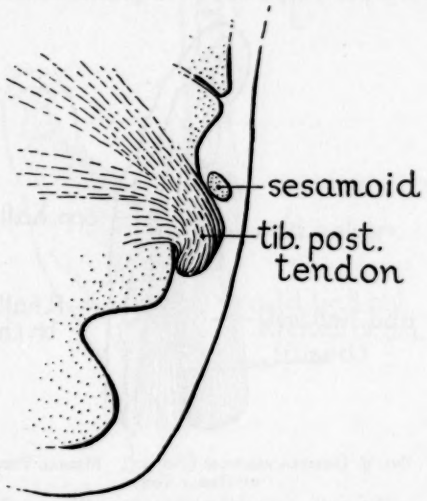


FIG. 8. GORILLA BERINGEI (No. 47). ARRANGEMENT OF TENDON OF TIBIALIS POSTERIOR ON PLANTAR SURFACE OF FOOT

× ⅓ natural size

into the tibial side of the base of the basal phalanx of the hallux and also into the metatarso-phalangeal joint capsule of the great toe. A few muscle fibres from the inner head are also inserted into the neck of the shaft of the first metatarsal bone, thus forming a rudimentary and quite feeble *opponens hallucis* (fig. 9). The fibular head of the *flexor hallucis brevis* is not a distinct muscle, but is united with the oblique portion of the *adductor hallucis*.

At first glance these two muscles appeared to be completely fused, so that I first obtained the impression that the fibular head of the *flexor hallucis* was absent, and that the *adductor hallucis obliquus* received a double nerve-supply, from each of the plantar nerves. Further investigation proved plainly that this was not the case. The inner (tibial) portion of this compound muscle, the portion which received the nerve from the N. *plantaris medialis*, was easily separated on its plantar surface

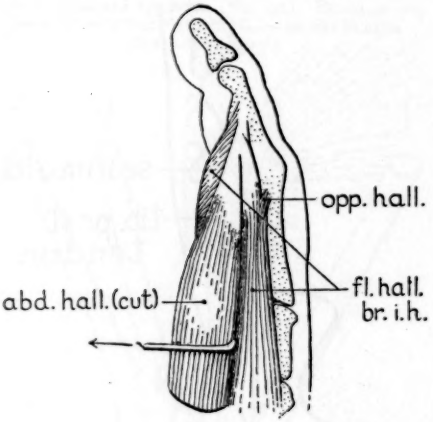


FIG. 9. GORILLA BERINGEI (No. 47). MEDIAL VIEW OF GREAT TOE

abd. hall. = abductor hallucis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *opp. hall.* = opponens hallucis. × approx. ⅔ natural size.

from the rest of the muscle, which was found to be innervated by the N. *plantaris lateralis*. A strong sheet of muscle, extending from the proximal end of the flexor to the distal end of the adductor element, unites the two muscles. On the dorsal surface, no natural separation of the compound muscle into its flexor and adductor components is to be found. I am therefore disposed to consider the tibial element, arising from the first and second cuneiform bones and sheath of the *peroneus longus*, and supplied by the medial plantar nerve, as representing the fibular head of the *flexor hallucis;* the fibular portion, which takes origin from the bases and proximal parts of the shafts of the third and second metatarsals, the interosseous fascia, and sheath of the *peroneus longus*, and which receives branches of the lateral plantar nerve, must then be the true oblique head of the *adductor hallucis*. It seems more logical to regard this doubly-innervated muscle mass in this manner, rather than simply as an *adductor obliquus* with dual nerve supply, especially since the usual fibular head of the *flexor hallucis brevis* is not otherwise represented. But because of the complete dorsal fusion and the occurrence of the plantar connecting muscle-sheet, it is of course impossible to say just where one muscle ends and the other begins. The tibial head of the *flexor hallucis brevis* is larger than the muscle-mass which represents the fibular head. *Innervation:* the tibial head of the *flexor brevis* is supplied by branches of the medial plantar nerve; the fibular head, as already stated, receives its nerve-supply from the same nerve.

M. adductor hallucis (*M. contrahens I*) (figs. 10, 11). This is a large and powerful muscle. It is clearly divided into transverse and oblique heads. The transverse head (*M. transversalis pedis* of older authors) arises from the proximal parts of the heads and most distal parts of the shafts of the fourth, third and second metatarsals, from the joint-capsules and transverse metatarsal (capitular) ligaments of these bones, from the fascia over the intervening interosseous muscles, and also slightly from the deep slips of the fibular portion of the plantar aponeurosis. The oblique head arises from the bases of the third and second metatarsals, from the fascia over the intervening interosseous muscles, from the sheath of the *peroneus longus* and *cuneiformia I* and *II*. This

oblique head contains the fibular head of the *flexor hallucis brevis* (see previous section dealing with the latter muscle). The transverse head inserts fleshily into the fibular side of the base of the basal phalanx of the hallux, the metatarso-phalangeal joint-capsule of that toe, and dorsally into the head and neck of the shaft of *metatarsale I*. In addition, it gives off muscular slips which insert higher up in the fibular side of the first phalanx. The insertion on the first metatarsal bone extends for a considerable distance (about 1.5 cm.). The oblique head (including the fibular head of the *flexor hallucis brevis*), inserts fleshily into the hallucal metatarso-phalangeal joint-capsule in common with the fibres of the transverse head. *Innervation:* both the transverse and oblique heads are supplied by branches from the deep ramus of the lateral plantar nerve. The oblique receives, in addition, a branch from the medial plantar nerve; this nerve supplies the more tibial portion of the muscle, which I regard as representing the fibular head of the *flexor hallucis brevis*, fused with the true *adductor obliquus*.

I have found no certain traces of other elements of the adductor layer of muscles (i.e., *Mm. contrahentes II, IV, V*). There was a tough aponeurotic sheet covering the more lateral interosseous muscles on their plantar aspect, but this cannot with any certainty be interpreted as vestiges of the lateral contrahentes. In the orang-utan, Ruge (1878b) and I have found the lateral contrahentes in a vestigial condition, represented by a tough tendon-plate with extensions to the lateral digits. Their identity can be established by the course of

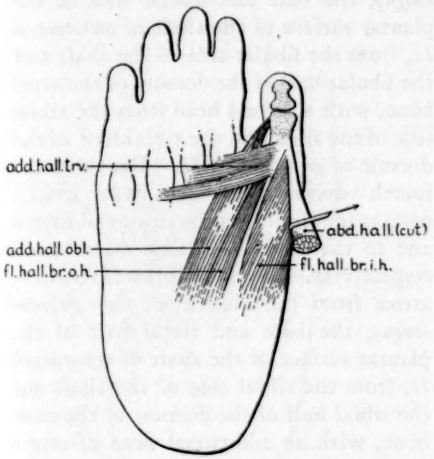


FIG. 10. GORILLA BERINGEI (No. 47). SHORT PLANTAR MUSCLES OF GREAT TOE

abd. hall. = abductor hallucis; *add. hall. obl.* = oblique head of adductor hallucis; *add. hall. trv.* = transverse head of adductor hallucis; *fl. hall. br. i. h.* = tibial head of flexor hallucis brevis; *fl. hall. br. o. h.* = fibular head of flexor hallucis brevis. × approx. ¼ natural size.

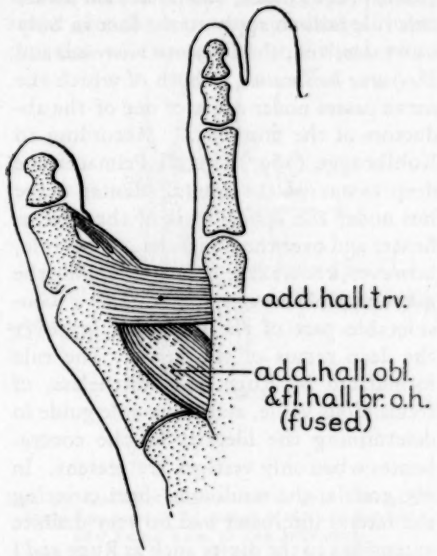


FIG. 11. GORILLA BERINGEI (No. 47). DORSAL VIEW OF ADDUCTOR HALLUCIS

add. hall. obl. = oblique head of adductor hallucis; *add. trv.* = transverse head of adductor hallucis; *fl. hall. br. o. h.* = fibular head of flexor hallucis brevis. × approx. ½ natural size.

the deep division of the lateral plantar nerve, which separates this tendon-plate and the *adductor hallucis* from the deeper interosseous muscles. Ruge demonstrated that a separation of contrahentes (including of course the contrahens of the hallux, or *adductor hallucis*) and interossei by the deep ramus of the lateral plantar nerve is constant among mammals. Cunningham (1882, p. 136) states, "So far as I am aware this rule fails to apply to the foot in only two cases, viz., the *Dasyurus viverrinus* and *Dasyurus hallucatus*, in both of which the nerve passes under cover of one of the abductors of the minimus." According to Kohlbrugge (1897), in all Primates the deep ramus of the lateral plantar nerve lies under the aponeurosis of the contrahentes and over the interossei. This rule, however, knows exceptions, for among the gibbons Kohlbrugge found that a considerable part of the interossei lay over the deep ramus of the nerve. The rule formulated by Ruge is, nevertheless, of tremendous value, and is our sole guide in determining the identity of the contrahentes when only vestiges are present. In my gorilla, the tendinous sheet covering the lateral interossei had no very definite extensions to the digits such as Ruge and I found in the orang, and no portion of it was over (plantar to) the main trunk of the deep ramus of the lateral plantar nerve. It lay entirely distal to the main trunk of this nerve. I am therefore not at all certain that this sheet should be regarded as constituting degenerated elements of the contrahens layer. It is of course possible to consider this aponeurosis as constituting the distal portion of the degenerated outer part of the layer of contrahentes, and the proximal portion as having entirely disappeared. Such an assumption would explain the position of the nerve in respect to this sheet.

Mm. interossei dorsales et plantares (figs. 12, 13, 14). There are four dorsal and three plantar interosseus muscles. These muscles arise as in man, the dorsal muscles by two heads, the plantar by one. Two of the dorsal set are inserted on the second toe, one on each side of that digit; the remaining members of this series are inserted on the fibular sides of the third and fourth toes. The second dorsal interosseus arises from the sheath of the *peroneus longus*, the base and fibular half of the plantar surface of the shaft of *metatarsale II*, from the fibular side of the shaft and the fibular half of the dorsum of the same bone, with a second head from the tibial side of the shaft and the tibial half of the dorsum of *metatarsale III*. The third and fourth dorsal interossei have similar origins in relation to the third and fourth and to the fourth and fifth metatarsals, respectively. The first dorsal interosseus arises from the sheath of the *peroneus longus*, the base and tibial half of the plantar surface of the shaft of *metatarsale II*, from the tibial side of the shaft and the tibial half of the dorsum of the same bone, with an additional head of origin from the fibular side of the dorsum of the first cuneiform bone. In addition the first dorsal interosseus exhibits a sort of accessory slip, of good size, arising from the plantar surface of *metatarsale II*, from the interval between the main muscle-masses of the first and second dorsal interossei. This slip goes to the tibial side of the basal phalanx of the second toe and joins the main tendon of insertion of *dorsal interosseus I*. It seems undoubtedly to be a detached portion of the first dorsal interosseus (figs 12, 13, 14). The dorsal interossei insert into the sides of the bases of the basal phalanges of their respective digits, and send seemingly slight extensions into the extensor aponeuroses.

The plantar interossei are inserted into the tibial sides of the bases of the basal

phalanges of the third, fourth and fifth toes, with seemingly slight extensions into the extensor aponeuroses. Their origins are similar to those of the dorsal set, although of course limited to a single metatarsal bone. They therefore have but single heads of origin. The first plantar interosseus arises from the sheath of the *peroneus longus*, the base and tibial half of the plantar surface of the shaft of

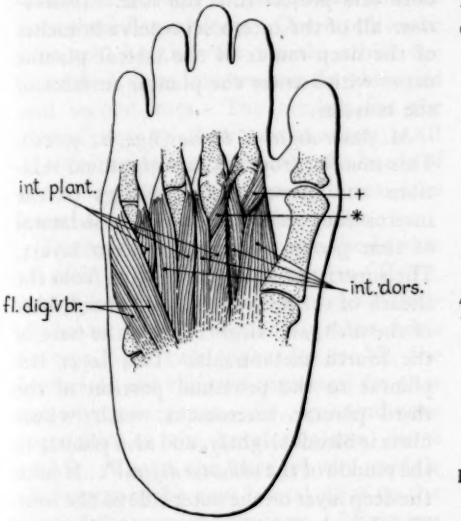


FIG. 12. GORILLA BERINGEI (No. 47). PLANTAR VIEW OF THE INTEROSSEOUS MUSCLES

fl. dig. V br. = flexor digiti V brevis; *int. dors.* = dorsal interossei; *int. plant.* = plantar interossei; + = slip to first dorsal interosseus; * = accessory muscle to second and third toes. × approx. ⅓ natural size.

metatarsale III, and from the tibial side of the shaft of that bone. The two remaining plantar muscles have similar relations to *metatarsalia IV* and *V*. The interossei arising entirely or in the main from any one metatarsal are not clearly separated in regard to their origins on the proximal part of the plantar surface of the bone, so that each pair of interossei for a single toe arise primarily from a common plantar muscle-mass. In the case of the third plantar interosseus, this has a common origin with the *flexor digiti V brevis*.

Intimately connected with interossei, there occurs a curious small muscle, which arises from the plantar surface of *metatarsale III*, from the interval between the first plantar and third dorsal muscles, just proximal to the head of the bone. This muscle divides into two parts, which insert into the metatarso-phalangeal joint capsules of the second and third toes,

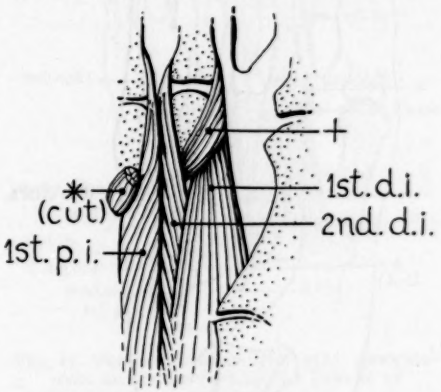


FIG. 13. GORILLA BERINGEI (No. 47). DETAIL TO SHOW RELATION OF ACCESSORY MUSCLE OF SECOND AND THIRD TOES TO THE INTEROSSEI

d. i. = dorsal interosseus; *p. i.* = plantar interosseus. The other symbols are the same as in the previous figure. × approx. ⅔ natural size.

plantar to the insertions of the interossei (figs. 12, 13). I could find no separate nerve for this muscle, which lies beneath (dorsal to) the deep ramus of the lateral plantar nerve. It is significant that I have found an identical muscle in the foot of the juvenile female gorilla (also *Gorilla beringei*, No. 7), which I have examined; but because all of the superficial muscles and all of the nerves had been removed when first I saw this specimen, I was unable to ascertain its further relations. This muscle is probably a portion of the deepest

plantar layer of muscles, which forms the two sets of interossei and *flexor digiti V brevis* (the *Mm. flexores breves* of some of the more primitive mammals). Its nerve-supply would seem most probably to have been derived from the branch to one of the two interossei with which it is primarily related (first plantar and third dorsal). Moreover, it seems extremely likely that the muscle is merely a detached slip from the common muscle mass giving rise to these interossei.

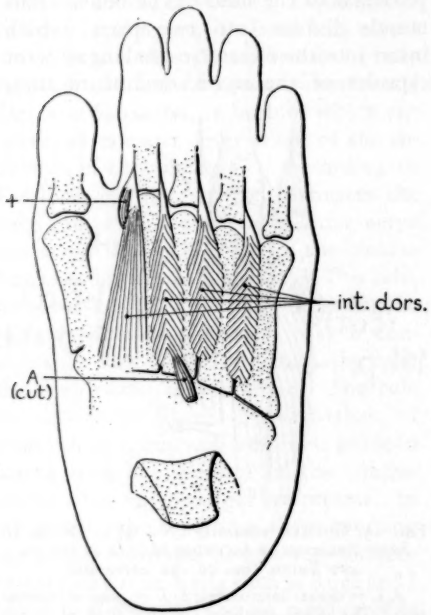


FIG. 14. GORILLA BERINGEI (No. 47). DORSAL VIEW OF THE INTEROSSEOUS MUSCLES

int. dors. = dorsal interossei; + = slip to first dorsal interosseus; *A* = accessory short extensor belly to second dorsal interosseus. × approx. ⅔ natural size.

The second dorsal interosseus also receives muscle fibres from the short extensor muscles on the back of the foot in the form of a small accessory belly (figs. 14, 17).

The interossei of this gorilla foot are thus arranged as in the foot of man, so that the dorsal set acts partly as abductors of the toes from an axis running through the mid-line of the second digit, while part of the function of the plantar set is to adduct the toes towards this imaginary axis. A similar arrangement existed in the other specimen of *Gorilla beringei* (No. 7) which I studied. Only the dorsal series can be seen from the dorsum of the foot, while both sets project into the sole. *Innervation:* all of the interossei receive branches of the deep ramus of the lateral plantar nerve which enter the plantar surfaces of the muscles.

M. flexor digiti V brevis (figs, 2, 3, 12). This muscle, from its topographical relations and nerve-supply, belongs to the interosseous series, being the most lateral of that group. It arises in two layers. The superficial layer has origins from the sheath of the *peroneus longus*, cuboid, base of the fifth, and slightly from the base of the fourth metatarsals. This layer lies plantar to the proximal portion of the third plantar interosseus, with whose fibres it blends slightly, and also plantar to the tendon of the *abductor digiti V*. It joins the deep layer on the outer side of the foot. The deep layer arises from the sheath of the *peroneus longus*, the proximal portion of the fibular half of the plantar surface of the shaft and from the base of *metatarsale V*, and from the proximal three-quarters of the fibular side of the shaft and distal portion of the tuberosity of that bone. The tendon of the *abductor digiti V* pierces the muscle in a manner which separates the superficial from the deep portion. The combined layers insert by a rather broad and flat tendon into the fibular side of the basal phalanx of the fifth toe, with a slight extension into the extensor aponeurosis. *Innervation:* from the deep division of the lateral plantar nerve.

M. opponens digiti V. This muscle is absent.

Muscles of the Dorsum of the Foot

M. extensor hallucis longus (figs. 15, 17). The insertion is by a broad flat tendon into the base of the terminal phalanx of the great toe, with a slight expansion at the base of the basal phalanx on each side of the tendon of the *extensor hallucis brevis*.

M. extensor digitorum longus (figs. 15, 17). The main tendon of this muscle divides into three flat tendons. One supplies the fifth toe, another the fourth, while the third re-divides into tendons for the third and second toes. The tendon for the second toe is smaller than the others. All of these tendons expand over the heads of their respective metatarsal bones into broad aponeuroses over the digits.

The extensor aponeurosis on the dorsum of each of the four lateral toes (II–V), which is formed by tendons of the *extensor digitorum longus*, *extensor digitorum brevis* (except in the case of that for toe V), the lumbrical and the two interossei for that toe, inserts as in man,—i.e., by a tendinous expansion to the basal phalanx, by a middle slip to the base of the middle phalanx, and by two lateral slips to the base of the terminal phalanx. I have not been able to trace out completely the various components of the extensor aponeurosis in my gorilla, probably because it had long been preserved. (Willan (1912) states that the distinction between the various tendons and the ensheathing aponeurotic sheet can be most easily demonstrated in fresh specimens.) In addition, these aponeuroses had been considerably injured in the process of skinning.

M. peroneus tertius (fig. 15). This muscle was already laid bare and dissected when I received the foot. The relations when seen by me were as follows:—The tendon inserts into the outer side of the base and proximal portion of the shaft of the fifth metatarsal bone by a tendinous sheet, inserting as two layers. Its association with the *extensor digitorum longus* is plainly shown by its fascial connections, the tendons of the two muscles being united by a very tough fascia.

M. tibialis anterior (figs. 15, 16). The insertion is by three definite tendons. The most anterior tendon curves around the inner border of the foot to insert on the plantar surface of the base of the metatarsal of the hallux. The middle and posterior tendons are at first joined, then split before their insertions. The middle tendon curves around the inner border of the foot and inserts by a broad expansion into the inner surface of the first cuneiform.

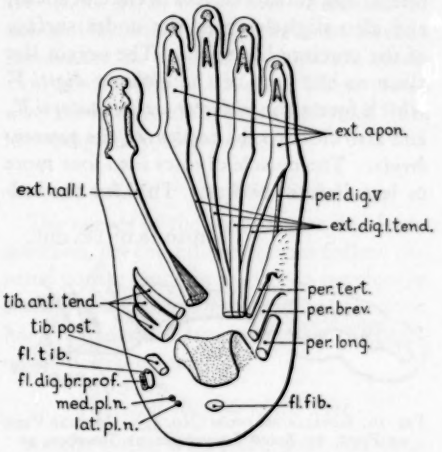


FIG. 15. GORILLA BERINGEI (No. 47). ARRANGEMENT OF THE TENDONS ON THE DORSUM OF THE FOOT

ext. apon. = extensor aponeuroses; *ext. dig. l. tend.* = tendons of extensor digitorum longus; *ext. hall. l.* = extensor hallucis longus; *fl. dig. br. prof.* = deep head of flexor digitorum brevis; *fl. fib.* = tendon of flexor fibularis; *fl. tib.* = tendon of flexor tibialis; *lat. pl. n.* = lateral plantar nerve; *med. pl. n.* = medial plantar nerve; *per. brev.* = tendon of peroneus brevis; *per dig. V* = vestige of peroneus digiti V; *per. long.* = tendon of peroneus longus; *per. tert.* = tendon of peroneus tertius; *tib. ant. tend.* = tendons of tibialis anterior; *tib. post.* = tendon of tibialis posterior. × approx. ½ natural size.

The posterior tendon also curves around the inner border and ends on a large sesamoid bone just distal to the tuberosity of the *naviculare*.

Mm. extensores hallucis et digitorum breves (figs. 3, 17). These muscles are in reality merely more or less marked divisions of a single muscle, which arises from the lateral and dorsal surfaces of the calcaneus, and also slightly from the under surface of the cruciate ligament. The origin lies close to the part of the *abductor digiti V* which forms the *abductor ossis metatarsi V*, and also close to the tendon of the *peroneus brevis*. The muscle divides into four more or less distinct bellies. That for the hallux is quite distinct because of its oblique course towards the great toe; it forms the part commonly known as the *M. extensor hallucis brevis*, which inserts into the basal phalanx of the hallux by a broad tendinous expansion. The remaining bellies insert into the fibular sides of the extensor aponeuroses of the tendons of the *extensor digitorum longus*, and form parts of these aponeuroses for the second, third and fourth toes. There is no short extensor tendon for the fifth toe. An additional muscle-belly, already mentioned in connection with the dorsal interossei, arises as a continuation of that portion of the muscle which forms the bellies for the first and second toes, but chiefly from the former. This little muscle is prolonged into the second dorsal interosseus, its fibers being continuous with those of the latter (figs. 14, 17). *Innervation:* the *extensores hallucis et digitorum breves* receive branches of the deep peroneal nerve. There is no separate nerve for the accessory muscle-belly running to the *dorsal interosseus II;* perhaps it receives its fibres from one of the other branches, in the substance of the muscle itself.

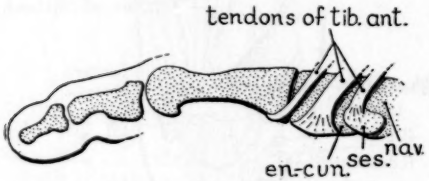


FIG. 16. GORILLA BERINGEI (No. 47). MEDIAL VIEW OF FOOT, TO SHOW INSERTIONS OF TENDONS OF TIBIALIS ANTERIOR

tib. ant. = tibialis anterior; *en.—cun.* = cuneiforme I; *nav.* = naviculare; *ses.* = para-naviculare sesamoid. × approx. $\frac{2}{3}$ natural size.

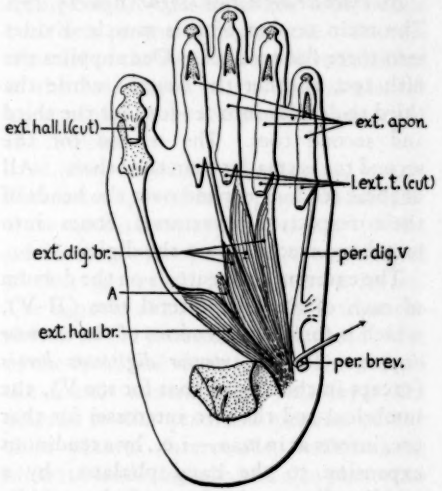


FIG. 17. GORILLA BERINGEI (No. 47). DORSUM OF FOOT TO SHOW SHORT EXTENSOR MUSCLES

ext. apon. = extensor aponeuroses; *ext. dig. br.* = extensor digitorum brevis; *ext. hall. br.* = extensor hallucis brevis; *l. ext. t.* = tendons of extensor digitorum longus; *per. brev.* = tendon of peroneus brevis; *per. dig. V* = vestige of peroneus digiti V; *A* = accessory short extensor belly to second dorsal interosseus. × approx. $\frac{8}{10}$ natural size.

M. peroneus longus (figs. 15, 18). This is represented by a thick, rounded tendon, about twice the diameter of that of the *peroneus brevis*, and lying posterior to the latter. It reaches the plantar surface of the foot by descending just medial to the *abductor ossis metatarsi V*. Covered by a strong sheath it reaches the tibial side of the foot and inserts by a flattened tendon

into the fibular plantar surface of the base of the metatarsal of the great toe. In addition, during its course across the sole, it gives off a definite, narrow tendon to the outer dorsal surface of the cuboid, and the portion of the tendon lying in the peroneal sulcus of the cuboid is attached to this bone by a tough, tendinous plate. There is no sesamoid bone in the portion of the tendon lying over the outer side of the cuboid.

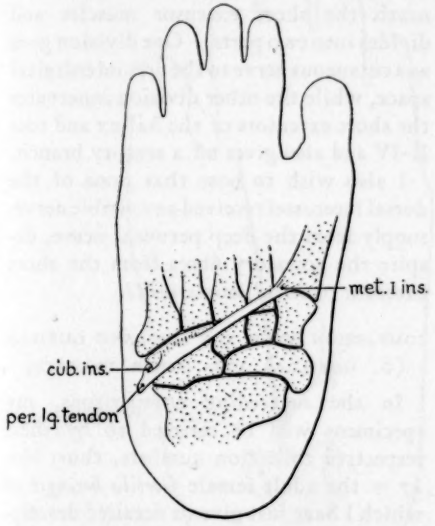


FIG. 18. GORILLA BERINGEI (No. 47). PLANTAR VIEW SHOWING TENDON OF PERONEUS LONGUS

cub. ins. = insertion of peroneus longus on cuboid; *met .I ins.* = insertion of peroneus longus on metatarsale I; *per. lg. tendon* = tendon of peroneus longus. × approx. ⅔ natural size.

M. peroneus brevis (figs. 15, 17). The tendon of this muscle lies, in the ankle, anterior to that of the *peroneus longus*. The thick, rounded tendon flattens out at its insertion into the dorsal and outer sides of the tuberosity of the fifth metatarsal bone. In addition, the main tendon gives off, just prior to its insertion, a narrow, flat tendon which runs between the two layers of the insertion of the *peroneus tertius* and passes forward along the dorsum of *metatarsale V* to join the extensor tendon to digit V on its deeper surface (figs. 15, 17). This little tendon represents the vestiges of a *M. peroneus digiti V*.

Sesamoid bones. X-ray photographs of the foot, kindly taken by my colleague, Dr. E. C. Hill, show that there are no sesamoids, other than the one already mentioned in connection with the insertion of the *tibialis anterior*. These plates also show that all of the epiphysial lines are completely obliterated.

NERVES OF THE FOOT

The nerves of the foot require but little mention, for their distributions follow the usual course found in man. As previously stated, the skinned condition of the foot has prevented me from studying the cutaneous distribution.

Nerves of the Sole of the Foot

At the point where the foot has been severed from the leg, the two plantar nerves are already separate entities. They here lie posterior and internal to the *flexor tibialis* (fig. 15). The lateral plantar nerve is the more posterior and lies slightly external to the medial plantar nerve. Both nerves reach the sole under cover of the laciniate ligament.

Medial plantar nerve (fig. 19). Its course is along the inner border of the foot. Branches are first given off for the superficial head of the *flexor digitorum brevis* and *abductor hallucis*. Distal to these it divides into two main trunks, the medial of which innervates the tibial head of the *flexor hallucis brevis* and ends in a cutaneous branch near the tip of the hallux; the lateral trunk supplies branches to the fibular head of the *flexor hallucis brevis* (which is united to the *adductor hallucis obliquus*), the *lumbricales* of toes II, III and IV, and ends in

cutaneous branches over the base of the second toe and in the first interosseous space.

Lateral plantar nerve (fig. 19). From the point where it enters the planta on the inner border it curves over sharply toward the lateral side of the foot. From its main trunk it supplies the *abductor digiti V*, and then splits into its superficial and deep divisions. The superficial division is sensory except for a branch which innervates the lumbrical of toe V. The deep division curves inwards and deep, and lies between the *adductor hallucis* and the interosseous muscles. It innervates the *flexor digiti V brevis*, both heads of the *adductor hallucis*, and all of the interossei (both plantar and dorsal), and also gives off sensory branches. There was no anastomosis between the plantar nerves.

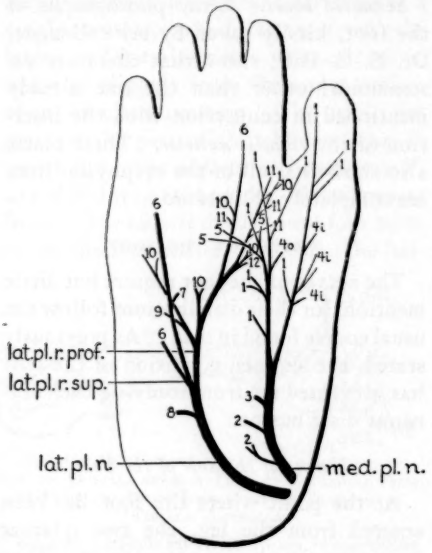


FIG. 19. GORILLA BERINGEI (No. 47). NERVES OF THE SOLE

med. pl. n. = main trunk of medial plantar nerve; *lat. pl. n.* = main trunk of lateral plantar nerve; *lat. pl. r. prof.* = deep division of lateral plantar nerve; *lat. pl. r. sup.* = superficial division of lateral plantar nerve; *1* = cutaneous branches of medial plantar nerve; *2* = to superficial head of flexor digitorum brevis; *3* = to abductor hallucis; *4i* = to tibial head of flexor hallucis brevis; *4o* = to fibular head of flexor hallucis brevis; *5* = to lumbricals of toes II, III and IV; *6* = cutaneous branches of lateral plantar nerve; *7* = to lumbrical of toe V; *8* = to abductor digiti V; *9* = to flexor digiti V brevis; *10* = to interosseous muscles; *11* = to adductor hallucis transversus; *12* = to adductor hallucis obliquus. × approx. ½ natural size.

Nerves of the Dorsum of the Foot

Deep peroneal nerve (fig. 20). It runs beneath the short extensor muscles and divides into two parts. One division goes as a cutaneous nerve to the first interdigital space, while the other division innervates the short extensors of the hallux and toes II–IV and also gives off a sensory branch.

I also wish to note that none of the dorsal interossei received any visible nerve-supply from the deep peroneal nerve, despite the accessory fibres from the short extensor to *dorsal interosseus II*.

COMPARISON WITH THE LOWLAND GORILLA (G. GORILLA) AND OTHER PRIMATES

In the succeeding comparisons, my specimens will be referred to by their respective collection numbers, thus: No. 47 = the adult female *Gorilla beringei* of which I have just given a detailed description; No. 7 = the juvenile female *G. beringei* in which I studied the interosseous muscles; No. 1105 = the infant female *G. gorilla* dissected by Dr. Morton, and on which I have made certain observations; and No. 5 = the infant female *G. gorilla* in which I noted the arrangement of the interosseous muscles.

Two important publications (Keith, 1899; Duckworth, 1915), in both of which the foot musculature of the lowland gorilla has been considered, are, unfortunately, of little use to me in the present study. Keith's paper gives some very interesting data on the variability of certain of the foot muscles, which are based upon accounts in the literature, and perhaps also

upon dissections of his own. He gives no bibliography, however, and since there is no way of determining his sources of information (most of which are undoubtedly also considered by me), I am therefore unable to make use of his data in the present more or less statistical study. For the same reason I am unable to include the information given by Duckworth. This obviously contains much original work, based upon dissections in the Cambridge University collection, but the author fails to discriminate completely between his own observations and those taken from the literature.

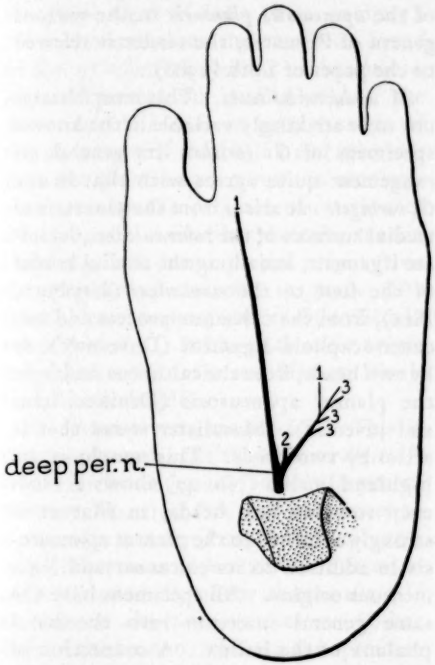


FIG. 20. GORILLA BERINGEI (No. 47). DEEP PERONEAL NERVE ON DORSUM OF THE FOOT

deep per. n. = deep peroneal nerve; *1* = cutaneous branches; *2* = to extensor hallucis brevis; *3* = to bellies of extensor digitorum brevis. × approx. $\frac{3}{8}$ natural size.

I have been unable to locate a copy of the important paper by Rothschuh (1888), so that my references to his studies on the muscles of the gorilla are cited from the papers of Sommer (1906) and Weidenreich (1922), chiefly from the former source. Likewise, both of the copies of the work of Eisler (1890) which were accessible to me were incomplete, and lacked the pages dealing with the nerves of the foot; my references to this paper have been taken from Kohlbrugge (1897).

The succeeding discussion is entirely limited to Primates. For a discussion of the complete foot musculature in all the groups of Tetrapods, the reader is referred to Ribbing (1909). McMurrich deals with the crural flexors (1904) and plantar muscles (1907) of Tetrapods. The papers of Glaesmer (1908 and 1910) cover the flexor musculature in mammals. Eisler's (1895a) important monograph is also most suggestive and of great interest. These are, naturally, only a few of the more important papers.

For the sake of uniformity, the Primate nomenclature followed in this paper is that of Elliot (1913). This, although not entirely satisfactory, is the best at the present time. When referring to a particular specimen, the author's terminology, if differing from that of Elliot, is given in parentheses. If succeeding reference is made to this specimen, only Elliot's terminology is given. Difficulties were, however, sometimes encountered in synonomyzing the names used by certain authors with those given by Elliot. For example, Kohlbrugge (1897) uses the name "*Semnopitheci*" as a collective term for his specimens of *Semnopithecus pyrrhus*, *S. maurus* and *S. nasicus*. These I have identified respectively as *Pygathrix aurata*, *P. cristata* and *Nasalis larvatus*. Elliot does not recognize the genus "*Semnopithecus*," and the sub-family "*Semnopithecinae*" he

terms "*Colobinae*." Since the three forms just mentioned are all included in the "*Colobinae*," I have substituted that name for Kohlbrugge's "*Semnopitheci*." It might also be mentioned that both *Semnopithecus pyrrhus* and *S. maurus* can be identified as *Pygathrix aurata*, but in order to avoid confusion I have called the latter *Pygathrix cristata*, for which it is also a synonym. There is, however, a strong possibility that both *Semnopithecus pyrrhus* and *S. maurus* are actually only varieties of a single species.

Aponeurosis plantaris. The only *aponeurosis plantaris* of a lowland gorilla for comparison with my highland gorilla is that of the young specimen described and figured by Loth (1908). In his animal apparently neither the metatarsal portion of the fibular part of the aponeurosis (*fasciculus fibularis*) nor the slip to the hallux (*fasciculus digiti I*) were as well-developed as in my animal. In other respects, however, the aponeuroses seem to have the same general arrangement. The differences in the fibular and hallucal parts of the structure might, at first glance, appear to constitute a difference between the highland and lowland types of gorilla. But Loth's work demonstrates that the exact form and development of the *aponeurosis plantaris* within a single genus of Primates is quite variable. This variability within a genus may or may not be connected with specific differences. At any rate, it indicates that any conclusions as to differences in the *aponeurosis plantaris* of such closely related forms as *Gorilla gorilla* and *G. beringei*, when based on such meagre material as that which is at present under consideration, mean very little, if anything. The strong development of the aponeurosis in my *G. beringei* strongly indicates an adaptation to a plantigrade mode of locomotion.

The *aponeurosis plantaris* sometimes (e.g., in *Galago*) occurs as merely a continuation of the tendon of the plantaris muscle over the *tuber calcanei* into the sole. The plantaris itself may be absent, as it usually is in the anthropoid apes (Kohlbrugge, 1897), and also occasionally in man, yet the aponeurosis always remains as a definite structure. For a most thorough account of the *aponeurosis plantaris* in the various genera of Primates, the reader is referred to the paper of Loth (1908).

M. abductor hallucis. This muscle seems not to be strikingly variable in the known specimens of *G. gorilla*. Its general arrangement quite agrees with that in my *G. beringei*. It arises from the plantar and medial surfaces of the *tuber calcanei*, laciniate ligament, and along the medial border of the foot to the *naviculare* (Hepburn, Pira); from the calcanear process and calcaneo-scaphoid ligament (Duvernoy); or by two heads, from the calcaneus and from the plantar aponeurosis (Deniker: fetus and juvenile). Macalister states that it arises by two heads. This muscle in the highland gorilla (No. 47) shows a tendency towards two heads, in that it is strongly attached to the plantar aponeurosis in addition to its calcanear and ligamentous origins. All specimens have the same general insertion into the basal phalanx of the hallux. A connection of the end tendon with the inner head of the *flexor hallucis brevis*, found in No. 47, is also mentioned by Duvernoy, Hepburn, and Pira.

The structure of the muscle is essentially similar in other Primates. In prosimians, e.g., in *Lemur* (Cunningham), *Lemur catta* (Murie and Mivart), and *Daubentonia* (*Chiromys*) *madagascariensis* (Zuckerkandl), it arises only from the plantar aponeurosis, and therefore has no bony origin.

M. abductor digiti V. This muscle is rather uniform in all gorillas, except that

in some its lateral fibres form an *abductor ossis metatarsi V*, which will be discussed below. The origins and insertions, when given, agree in general with the conditions in No. 47. Only Pira describes a partial origin from the fibular portion of the plantar aponeurosis; I found such an origin in No. 47. It may be united with the *flexor digiti V brevis* (Pira, Sommer). No author mentions the condition found in No. 47 where the tendon of the *abductor digiti V* pierces the muscle-belly of the *flexor digiti V brevis*. A partial origin of the abductors of the hallux and minimus from the plantar aponeurosis in monkeys demonstrates the original connection of these muscles with the plantaris tendon (Ribbing). It has a partial origin from the plantar aponeurosis in man. The muscle shows no noteworthy differences in other Primates. It has a calcanear origin in prosimians (Murie and Mivart, Woollard, Zuckerkandl).

M. abductor ossis metatarsi V. This is clearly a derivative of the *abductor digiti V*, with which it is usually united (Hepburn, Sommer, No. 1105, No. 47), but it may be a separate muscle (Pira). In Hepburn's animal there was apparently no separation of the muscle-belly of the *abductor digiti V* to form an *abductor ossis metatarsi V*, but only of the tendon, while in the specimen of Sommer and in Nos. 1105 and 47 the division extended into the muscle-mass itself. Bischoff, Deniker (2 specimens), Duvernoy, Hartmann and Macalister all state the *abductor digiti V* as being present in their gorillas, but none of these writers mention or picture any structure resembling an *abductor ossis metatarsi V*. I therefore feel justified in concluding that it was absent in their animals. An abductor of the fifth metatarsal therefore occurs in the single highland gorilla and in three of nine lowland gorillas (33.3 per cent). If the figures are united the frequency in gorillas is four out of ten (40 per cent). This muscle occurs in man in over 40 per cent of cases (Bryce). It may be a separate structure or a part of the abductor.

This muscle is often found in the chimpanzee (Kohlbrugge), and it was present in my specimen. It is, however, apparently rare in the orang (Le Double cites its presence in one specimen, but it was absent in my animal and in Hepburn's, while neither Kohlbrugge nor Sonntag note its occurrence). I find no reference to it in the gibbons, but it probably occurs at least occasionally in these animals. The abductor of the fifth metatarsal is present in some Old World monkeys, e.g., in my *Pygathrix germaini*, in Cunningham's *Papio papio* (*Cynocephalus sphinx*), and in the bonnet macaque (*Pithecus sinicus*), *Papio cynocephalus* (*Cynocephalus anubis*) and *Papio papio* (*Cynocephalus sphinx*) (Le Double). I have at hand no reference to it in New World monkeys, but it undoubtedly must exist in representatives of this group (Cunningham notes its absence in *Ateles* (?)). The muscle is frequent in prosimians, e.g. in my galago, in *Lemur catta*, *L. nigrifrons*, *Galago crassicaudatus* and *G. garnetti* (Murie and Mivart), in *Lemur* (Cunningham), in *Lemur variegatus* (*varius*) and *Galago* (*Otolicnus*) *crassicaudatus* (Zuckerkandl), in *Daubentonia* (*Chiromys*) *madagascariensis* (Oudemans), and in *Tarsius* (Woollard).

M. flexor digitorum brevis (fig. 21). In all gorillas (except those of Hepburn and Chapman) this muscle is composed of two heads: a superficial, arising from the calcaneus and plantar aponeurosis (Pira, Rothschuh, Sawalischin, Sommer, No. 47), or from the calcaneus alone (Bischoff, Deniker, Duvernoy, Huxley, Owen), and a deep head, arising on the plantar surface of the tendon of the *flexor tibialis* (Bischoff, Deniker, Duvernoy, Hartmann, Huxley, Owen, Pira, Rothschuh, Sawalischin,

Sommer, No. 47). In Hepburn's specimen there was only one head, arising chiefly from the calcaneus. Chapman's gorilla had really three distinct heads of origin, namely, a superficial, from the calcaneus, and two deep ones attached respectively to the tendons of the tibial and fibular flexors; the short flexor tendon for toe IV came from the tibial flexor, that for toe V from the fibular. The deep head would seem usually to be fleshy, occasionally a simple tendinous prolongation of the long flexor tendon, but not all writers make this point clear. In Table 1 I have arranged the findings of the various investigators to indicate the sources of origin of the tendons of the *flexor digitorum brevis* for the various toes. This table shows that in the lowland gorilla the tendons for the second and third digits usually arise entirely from the superficial head of the muscle, in a few cases that for the third may come partially from the deep head. The tendon for the fourth toe nearly always originates solely from the deeper layer, but in one animal wholly from the superficial. The tendon for the fifth digit, when present, is always a product of the deep head. In the single highland gorilla (No. 47) the condition is not exactly similar to that of any of the lowland gorillas, but it falls between the majority, in which the superficial layer supplies only the second and third toes, and Hepburn's specimen, in which all of the tendons arise from the superficial head alone, the deep head being absent. In Hepburn's animal the arrangement agrees with usual conditions in man.

TABLE 1

Sources of the short flexor (flexor digitorum brevis) tendons in gorillas. The superficial head in all instances arose from the calcaneus or from that bone and the plantar aponeurosis, the deep head always from the undivided flexor tibialis tendon, except in Chapman's specimen, in which the fifth toe tendon arose from that of the flexor fibularis

AUTHOR	SUPERFICIAL HEAD	DEEP HEAD
Bischoff	2 3	4 5
Chapman	2 3	4 5
Deniker (fetus)	1 2 3	4
Deniker (juvenile)	2 3	4 5
Duvernoy	2 3	4 5
Hartmann	2 3	4 5
Hepburn	2 3 4	
Huxley	2 3	4 5
Owen	2 3	4
Pira	2 3	4 5
Rothschuh	2 3	3 4
Sawalischin (a)	2 3	(3) 4
Sawalischin (b)	2 3	(3) 4 5
Sommer	2 3	4 5
No. 47	2 3 4	3 (4) 5

I have found the following arrangements of the *flexor digitorum brevis* in other animals. Chimpanzee: superficial head supplies the tendon for toe II and about half of that for III, the rest of the latter tendon and all of those for IV and V coming from the deep head. Orang: superficial head produces the tendon for II, about half of that for III, and the minor portion of that for IV, the remainder of the tendons for III and IV, and all of that for V, arising from the deep head. *Pygathrix germaini:* the tendon for II arises from the superficial head, those for III, IV and V from the deep. *Galago:* as in *Pygathrix*. In the chimpanzee and orang the superficial head arose from the calcaneus and partly from the plantar aponeurosis, in *Pygathrix* and *Galago* only from the aponeurosis. In all cases the deep head was associated with the undivided tendon of the *flexor tibialis*, and in *Pygathrix* also slightly with that of the *flexor fibularis*.

The tendon to the fifth toe, as already mentioned, is not always present. In addition to the cases listed above, Macalister noted its absence in his gorilla, and I found none in No. 1105. The short flexor

tendon to the fifth toe is therefore completely lacking in seven out of sixteen lowland gorillas. If we combine these cases with the single highland gorilla, in which it was vestigial, we find it lacking in 41.2 per cent of gorillas (seven out of seventeen). My gorilla, No. 47, shows a condition which may be interpreted as representing the short flexor tendon for toe V in the last stages of reduction. As already stated in the description of the *flexor fibularis* of No. 47, the terminal long flexor tendon for toe V gives off a tendinous slip which inserts on middle phalanx V in the manner of a short flexor tendon. Apparently this same tendon in Duvernoy's gorilla, judging from his description and illustration (plate X), was in a state of reduction similar to that exhibited by No. 47. Schwalbe and Pfitzner (1894) found the tendon to the little toe to be absent in Europeans of both sexes in 25 per cent (135 out of 540) of all feet examined. This tendon was absent in 24.4 per cent (161 out of 659) of Japanese feet (Adachi, 1910) and in 18.4 per cent (21 out of 114) of Negro feet (Loth, 1912).

Judging from accounts in the literature, this fifth toe tendon is not so frequently lacking in the chimpanzee, orang and gibbon as it is in the gorilla. Kohlbrugge's table shows it to have been absent in four out of thirteen chimpanzees (30.8 per cent); in three out of fourteen orangs (21.4 per cent); in three out of eight gibbons (37.5 per cent). I found it in both my chimpanzee and orang. Its absence in other Primates would seem to be a very rare occurrence. Sawalischin found it in all of her monkeys and prosimians. It was present in my *Pygathrix* and *Galago*. But Rothschuh found it absent in two baboons. It may be concluded that in the reduction of the *flexor digitorum* tendon to the fifth toe the gorilla, chimpanzee and gibbon have progressed further than has man, and the orang about as far. Of added significance is the fact that this reduction is practically confined to the anthropoids and man.

The fifth toe tendon may be imperforate in the gorilla (Chapman, Huxley). The vestigial tendons for this digit found in Duvernoy's animal and No. 47 were likewise not perforated. Lack of perforation of this tendon may also occur in other anthropoids (Kohlbrugge) and in man (Bryce).

An accessory flexor of the hallux, arising from the inside of the calcaneus between the origins of the *flexor digitorum brevis* and the *abductor hallucis*, and inserting by a long tendon into the basal phalanx of the great toe, was found by Deniker in his fetal gorilla. He homologizes this muscle, after its mode of termination, with the perforated tendons of the other toes. A similar muscle has been noted in the orang by Barnard (1875) and in *Tarsius* by Allen (1898). The "*fasciculus hallucis*" found by Sawalischin in *Pithecus irus* (*Macacus cynomolgus*) and *Lasiopyga* (*Cercopithecus*) *callitrichus*, and the "*flexor brevis hallucis superficialis*" of *Tarsius* (Burmeister, Woollard) would also seem to be homologous structures.

In order to understand the condition of the *flexor digitorum brevis* in the gorilla, it is necessary to survey briefly the morphology of this muscle. The researches of Ribbing (1909) indicate that the entire *flexor digitorum brevis* of mammals (i.e., both heads) should be regarded as a part of the outer flexor mass of the leg, and as representing the more superficial part of the *flexores breves superficiales* of amphibians and reptiles. It is not necessary to go into a lengthy discussion concerning its probable original condition in Tetrapods, i.e., whether it primarily consisted of a single superficial head or a single deep head, or was already divided into superficial and

deep layers. At least it is quite clear, from the investigations of Sawalischin and others, that within the order Primates there is a distinct tendency for the muscle to present a single superficial origin, and for the deep head to become eliminated. Whether the deep head has actually disappeared, or whether it has become united with the superficial head, or otherwise modified, are points which need not long detain us here (on these points see Weidenreich, 1922, S. 241–250). The available evidence indicates that, among the Primates at least, an actual transfer of the deep head from long flexor tendon to calcaneus and plantar aponeurosis has occurred phylogenetically. In other words, the deep head seems to exhibit a tendency to become united with the superficial. Notwithstanding the fact that the entire muscle shows individual variability in all the families of Primates, as would naturally be expected, its general characteristics in the various groups are quite apparent. Thus, in the usual condition among prosimians and monkeys the tendon for toe II is derived entirely from the superficial head (i. e., from the plantar aponeurosis or calcaneus, or from both), with the remaining toes (the hallux of course excepted) supplied solely from the deep head of the muscle (attached to the tendon of the *flexor tibialis* or to both long flexor tendons). There is also a tendency for the tendons for III and IV to arise in whole or part from the superficial head in a few prosimians and monkeys (Sawalischin). The condition in the gibbons is practically the same as in most monkeys and prosimians, in that nearly all specimens exhibit the superficial head supplying only the second toe (Glaesmer, Kohlbrugge, Sawalischin). In the three great apes, however, there is a much closer approach to the human condition, the tendons for both II and III being nearly always derived from the superficial head alone, and that for IV not infrequently. A superficial origin for the fourth toe tendon occurs most frequently by far in the orang (see Table 2). The tendon for the little toe apparently occurs as an element of the superficial layer only in man (large majority) and in the orang (occasionally). Very rarely in monkeys, as in Bischoff's anomalous *Callithrix* (*Hapale*) *penicillata*, and in one of Sawalischin's seven specimens of *Pithecus irus*, the fifth toe tendon may arise at least in part from the superficial head. As far as the

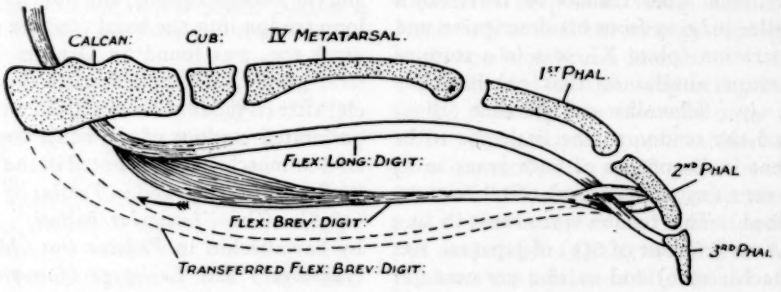


FIG. 21. SECTION OF THE FOOT OF A MONKEY THROUGH THE TARSUS AND FOURTH DIGIT, TO REPRESENT THE TWO ORIGINS OF THE FLEXOR DIGITORUM BREVIS MUSCLE

The arrow indicates the probable method of transference of the origin of the muscle from long flexor tendon to calcaneus. (After Keith, 1929.)

flexor digitorum brevis is concerned the orang more closely approaches man than do the chimpanzee and the gorilla. In man all of the short flexor tendons usually arise from the calcaneus, with a slight attachment to the under side of the plantar aponeurosis; the deep head is normally entirely absent (transferred to the calcaneus), but in a small percentage of cases it may be present in that the tendon for toe V may be derived in whole or part from a small muscle-belly associated with the undivided tendon of the *flexor tibialis*. This condition occurs in 11 per cent of cases (11 out of 100) according to Schulze (1867); in 10 per cent of cases (5 out of 50) according to Turner (1867); and in 5 per cent of cases according to Keith (1929). The work of Schulze and Turner was done on Europeans. As to the source of Keith's figure, I am unable to give information. In a small series of Negroes (twelve feet) I found the fifth toe tendon arising entirely from a small muscle-belly on the undivided *flexor tibialis* tendon (deep head) in four cases (33.3 per cent), entirely from the calcaneus and plantar aponeurosis (superficial head) in five cases (41.7 per cent), and completely absent in three cases (25 per cent). The tendon for toe IV may also have a partial deep origin in 2 per cent of Europeans (2 out of 100) according to Schulze, and in 8.3 per cent of Negroes (1 out of 12), according to my series. Similarly, the tendon for III may have a partial deep origin: in 1 per cent of Europeans (1 out of 100), according to Schulze; in 2 per cent of Europeans (1 out of 50), according to Turner; and in 8.3 per cent of Negroes (1 out of 12), according to my notes.

There is therefore, as already stated, a distinct tendency among Primates for the *flexor digitorum brevis* to assume a superficial origin. In the three great apes we see this muscle in stages intermediate between the conditions usual in monkeys and that

TABLE 2

Degree (per cent) of transference of origin of the separate digital tendons of the flexor digitorum brevis muscle from the tendon of the flexor tibialis muscle to the calcaneus and plantar aponeurosis, in some representative Primates. It should be noted that the transference begins at the inner side of the foot and progresses rather gradually towards the outer. The gorilla and chimpanzee have reached approximately the same stage in the evolution of the muscle, but the orang-utan, however, even more closely approaches the human condition (practically complete transference to calcaneus). This is a parallel specialization of the orang foot not found in its other muscles. Absence of a tendon has been regarded as non-transference. Based on data collected by the author from the literature and from his own dissections

	NO. SPEC.	TOE II			TOE III			TOE IV			TOE V		
		Partial Trans.	Complete Trans.	P. + C. Trans.	Partial Trans.	Complete Trans.	P. + C. Trans.	Partial Trans.	Complete Trans.	P. + C. Trans.	Partial Trans.	Complete Trans.	P. + C. Trans.
Man	69	0	100	**100**	3	97	**100**	4	96	**100**	0	78	**78**
Gorilla	15	0	100	**100**	27	73	**100**	7	7	**14**	0	0	**0**
Chimpanzee	28	4	93	**97**	79	18	**97**	29	0	**29**	0	0	**0**
Orang-utan	24	0	92	**92**	8	92	**100**	33	21	**54**	4	17	**21**
Gibbon	21	14	86	**100**	5	0	**5**	0	0	**0**	0	0	**0**
Pithecus	13	15	85	**100**	31	0	**31**	15	0	**15**	8	0	**8**
Pygathrix	13	23	77	**100**	8	0	**8**	0	0	**0**	0	0	**0**
Cebus	8	0	100	**100**	25	0	**25**	0	0	**0**	0	0	**0**
Callithrix	11	27	64	**91**	18	0	**18**	0	0	**0**	9	0	**9**
Galago	9	0	78	**78**	0	0	**0**	0	0	**0**	0	0	**0**

normally found in man, stages similar to those through which this muscle probably passed at some period of man's evolution.

If we express the transference of the origin of the tendons mathematically, we obtain some idea of the degree in which the gorilla approaches man. Thus, in the fifteen gorillas, the tendon for toe II always arises entirely from the calcaneus (and plantar aponeurosis); that for toe III has undergone complete transference to the calcaneus in 73.3 per cent (11 animals) and partial transference in the remaining 26.7 per cent (4 animals), so that in no specimen is this tendon derived wholly from the deep layer; the tendon for toe IV has entirely migrated in only 6.7 per cent (1 animal), and partially in 6.7 per cent (1 animal) also, while in the remaining 86.6 per cent (13 animals) no transfer has taken place. The tendon for V, whenever present, arises entirely from the deep head.

In the foot of a human embryo of 20 mm. C. R. length, Bardeen (1907) found the *flexor digitorum brevis* anlage associated with the surface of the aponeurosis of the long flexor muscles. This, it seems to me, suggests a primary connection of the short flexor of the toes with the long flexors. It offers an explanation for those cases in which part of the muscle arises from the long flexor tendon.

M. flexor tibialis and M. flexor fibularis (fig. 22). These muscles are most profitable considered together, for in the gorilla they are practically always more or less united in the sole, and a single digit is frequently supplied by both. The distribution of the tendons in the various specimens investigated is given in table 2. The hallux is supplied exclusively by the fibular flexor in all of the lowland gorillas, but in the highland gorilla (No. 47) most of the great toe tendon is derived from the tibial flexor. The second toe is usually supplied by the tibial flexor alone (Chapman, Deniker: fetus, Deniker: juvenile, Duvernoy, Hartmann, Hepburn, Huxley, Owen, Rothschuh, Sommer), but sometimes by both flexors (Bischoff, Macalister, No. 47), or by the fibular flexor alone (Pira). Usually the third toe tendon is derived only from the *flexor fibularis* (Bischoff, Chapman, Deniker: fetus, Deniker: juvenile, Duvernoy, Hartmann, Hux-

TABLE 3

Distribution of the long flexor muscles in gorillas, with reference to the origin of the long flexor tendons

AUTHOR	FLEXOR FIBULARIS	FLEXOR TIBIALIS
Bischoff	1 2 3 4 5	2 5
Chapman	1 3 4	2 5
Deniker (fetus)	1 3 4	2 5
Deniker (juvenile)	1 3 4 5	2 5
Duvernoy	1 3 4	2 5
Hartmann	1 3 4	2 5
Hepburn	1	2 3 4 5
Huxley	1 3 4	2 5
Macalister	1 2 3 4	2 3 4 5
Owen	1 3 4	2 5
Pira	1 2 3 4	5
Rothschuh	1 3 4	2 3 4 5
Sommer	1 (5)	2 3 4 5
No. 47	(1)(2) 3 4 5	1 2(3)(4)

ley, Owen, Pira), but it may be supplied by both flexors (Macalister, Rothschuh, No. 47), or from the *flexor tibialis* alone (Hepburn, Sommer). The fourth toe tendon is also customarily derived from the *flexor fibularis* (Bischoff, Chapman, Deniker: fetus, Deniker: juvenile, Duvernoy, Hartmann, Huxley, Owen, Pira), but it may come from both flexors (Macalister, Rothschuh, No. 47), or only from the *flexor tibialis* (Hepburn, Sommer). The fifth toe is nearly always provided for by the tibial flexor solely (Chapman, Deniker: fetus, Duvernoy, Hartmann, Hepburn, Huxley, Macalister, Owen, Pira, Rothschuh), or by both flexors (Bischoff, Deniker: juvenile, Sommer), or else by the fibular flexor entirely (No. 47). It will be noted that the *flexor fibularis* tends to supply the first, third and fourth toes exclusively, while the *flexor tibialis* is confined to the second and fifth toes. A similar arrangement is found in most chimpanzees and orang-utans (Kohlbrugge), although in the latter ape the long flexor tendon for the hallux is nearly always missing, this probably being a degenerative specialization which is merely a manifestation of the reduction of that digit in the orang. But the distribution of the long flexor tendons in the great apes can hardly be as simple as the tables of Kohlbrugge (S. 202–203) and myself (table 3) indicate. While there are, of course, many cases among the anthropoids in which no connection between the long flexors occurs (in my orang there was no connection whatsoever between the tendons, the fibular supplying III and IV and the tibial II and V; also see Glaesmer, 1910, on this point), yet, in the gorilla at least, this is by no means the rule (in my chimpanzee the fibular flexor supplied all of the tendon for I and the major portions of those for III and IV, the tibial all of those for II and V, and sent a strong slip to augment the fibular tendons for III and IV). Thus, Chapman, Deniker, Duvernoy, Hartmann, Hepburn, Huxley, Pira and Sommer all note that the long flexors of their gorillas have tendinous connections in the sole,—findings which of course can only mean that some of the digits were supplied by both flexors. Yet none of these writers indicates a dual tendon supply for any of the toes (except for the fifth toe in Deniker's juvenile and Sommer's gorilla). There can be but little doubt that the distribution of the long flexor tendons in all of these animals was much more complex than the accounts of the investigators indicate. In the gorillas of Bischoff, Macalister and Rothschuh, and in No. 47, some of the lateral toes receive tendinous elements from both long flexors. Owen indicates the usual simple anthropoid ape type of distribution, and does not mention any connection between the tendons. As already stated, Kohlbrugge's table indicates that in the three great apes the *fl. fibularis* is usually confined to toes I, III and IV, and *fl. tibialis* to II and V (that for I not normally occuring in the orang). But, I would repeat, there is evidence that a mingling of fibres of the two primary flexor tendons occurs very frequently (as in my chimpanzee), and this is certainly the case in nearly all gorillas.

In man, the *fl. fibularis* (*fl. hallucis longus*) has concentrated chiefly upon the hallux, while the *fl. tibialis* (*fl. digitorum longus*) is divided to the four lateral toes, and only occasionally contributes to the formation of the hallucal tendon. Schulze (1867) and Turner (1867) studied the distribution of the long flexor tendons in Europeans in 100 and 50 examples respectively. Schulze found that the *flexor fibularis* always supplied the hallux and the second digit. It went to toes I and II alone in 32 per cent (32 cases); to I, II and III in 58 per cent

(58 cases); and to I, II, III and IV in 10 per cent (10 cases). He found the *flexor tibialis* always supplying the three outer digits. It contributed to the tendon for toe II in 98 per cent (98 cases), and to that for the hallux in 29 per cent (29 cases). The hallucal tendon, therefore, was in 71 per cent supplied by the *fl. fibularis* alone, in 29 per cent by both muscles; the tendon for II in 2 per cent by the *fl. fibularis* only, in 98 per cent by both flexors, the tendon for III in 32 per cent by the *fl. tibialis* alone, in 68 per cent by both; the tendon for IV solely by the *fl. tibialis* in 90 per cent, by both in 10 per cent; and the tendon for V in 100 per cent by the *fl. tibialis* alone. Turner obtained essentially similar results. In his group the *flexor fibularis* always went to the first and second digits. It went to toes I and II alone in 22 per cent (11 cases); to I, II and III in 40 per cent (20 cases); to I, II, III and IV in 36 per cent (18 cases); and to I, II, III, IV and V in 2 per cent (1 case). The *flexor tibialis* in every instance sent fibres to III and IV, and in 98 per cent (49 cases) to V. In the one foot in which the tibial flexor failed to reach the fifth toe, the perforating tendon of that digit was derived entirely from the *quadratus plantae*. The *fl. tibialis* likewise supplied toe II in 96 per cent (48 cases), and toe I in 18 per cent (9 cases). The tendon to the hallux, therefore, was supplied solely by the *fl. fibularis* in 82 per cent, by both flexors in 18 per cent; the tendon for II in 4 per cent by the *fl. fibularis* only, in 96 per cent by both; the tendon for III in 22 per cent by the *fl. tibialis* alone, in 78 per cent by both; the tendon for IV by the *fl. tibialis* by itself in 62 per cent, by both in 38 per cent; and the tendon for V in 96 per cent by the *fl. tibialis* alone, in 2 per cent by both. In the twelve Negro feet which I studied the *fl. fibularis* always went to the two tibial digits. It supplied toes I and II only in 25 per cent (3 cases); I, II and III in 58.3 per cent (7 cases); I, II, III and IV in 16.7 per cent (2 cases). The *fl. tibialis* always supplied the three fibular digits. It also went to toe II in 91.7 per cent (11 cases). The great toe tendon therefore received fibers only from the *fl. fibularis* (100 per cent); the tendon for II only from the *fl. fibularis* in 8.3 per cent, from both flexors in 91.7 per cent; the tendon for III solely from the *fl. tibialis* in 25 per cent, from both in 75 per cent, the tendon for IV only from the *fl. tibialis* in 83.3 per cent, from both in 16.7 per cent; and the tendon for V always solely from the *fl. tibialis* (100 per cent). These results agree essentially with those obtained by Schulze and Turner on Europeans. Although my present series is quite small, I have thought it worth while to include it here, since it is composed entirely of Negroes. In man, therefore, there is a decided tendency for the *fl. fibularis* to become restricted to the hallux, and for the *fl. tibialis* to assume control of the other toes. The tibial flexor has not as yet, however, begun to eliminate the fibular element in the second digit. The usual human type of arrangement of the long flexor tendons is not normally found in any other Primate. Macalister's gorilla, however, exhibits an arrangement not infrequent in man. The distribution of the tibial flexor in my chimpanzee somewhat suggests the usual arrangement in man. In most gibbons the fibular flexor is distributed to the four inner toes, the tibial flexor being confined chiefly to the second and fifth, but it may also contribute to the formation of other tendons, notably that to the hallux (Kohlbrugge, Glaesmer). In both man and gibbon the tendon to the hallux not infrequently contains a tibial element, and that to the second toe always contains fibular fibres. These are primitive characters, in contrast to the arrangements for

these toes in the three great apes. Some monkeys show a definite approach to the anthropoid ape type of arrangement, the *flexor fibularis* supplying toes I, III and IV and the *flexor tibialis* II and V. But in practically all monkeys, as in gibbons and prosimians, the hallucal tendon is derived from both muscles, and other digits (notably the fourth) often receive a double supply also (Pagenstecher, Kohlbrugge, Glaesmer). In *Pygathrix germaini* I found the *fl. fibularis* supplying all of the tendons for III and IV, and that for I in common with the *fl. tibialis* and *quadratus plantae*, which muscles also furnish the tendons for II and V. There was no other connection between the long flexor tendons. In most of the prosimians both long flexors are usually rather evenly distributed, the four inner digits usually receiving a dual tendon-supply, (Murie and Mivart, Zuckerkandl, Glaesmer, Straus) while the fifth toe tendon may be from the *fl. tibialis* alone (Zuckerkandl, Glaesmer, Straus), or from both flexors, but chiefly from the tibial (Murie and Mivart, Zuckerkandl). In *Galago* I found the *fl. tibialis* going to all the toes, the *fl. fibularis* to all except the fifth. Zuckerkandl found a quite advanced condition in his specimens of *Daubentonia madagascarensis* and *Galago crassicaudatus*. In these animals the long flexor tendon of the hallux was derived from the *flexor fibularis* alone, while all of the other toes were supplied by both flexors.

It is generally agreed that the fibular and tibial flexors of mammals have been derived phylogenetically from different muscle layers (Eisler, 1895a; McMurrich, 1905; Ribbing, 1909). Both Dobson (1883) and Glaesmer (1910) regard the plantar fusion of the two long flexors as the primitive mammalian condition, and their separation as secondary. The opposite view is maintained by Ribbing. The prosimians therefore essentially exhibit what Dobson and Glaesmer regard as a primitive condition, with other Primates showing more advanced arrangements. The fusion of the tendons and their mode of distribution in the highland gorilla (No. 47) suggest the type of arrangement in prosimians and some monkeys.

I do not believe that, among the great apes, the long hallucal flexor tendon has

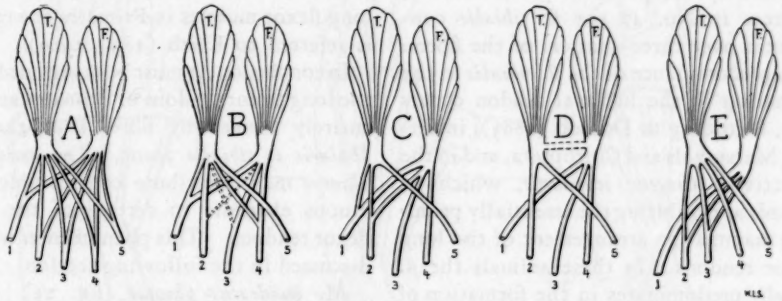


FIG. 22. DIAGRAMMATIC REPRESENTATION OF VARIOUS TYPES OF DISTRIBUTION OF THE TENDONS OF THE FLEXOR TIBIALIS (*T.*) AND FLEXOR FIBULARIS (*F.*) MUSCLES IN PRIMATES

A. Most prosimians. B. Most monkeys. C. Most gibbons. D. Most orang-utans, chimpanzees and gorillas (in nearly all orangs, however, the tendon to the hallux is absent). E. Usual arrangement in man. The connecting band, shown by dashed lines, which unites the primary long flexor tendons in diagram D, indicates that one or more of the tendons for the four lateral digits may at times receive fibers from both muscles.

hitherto been observed to be composed of fibres from both long flexors. This is an arrangement characteristic of the gibbons, monkeys and prosimians (it occasionally occurs, as already cited, in man). Yet even in these animals (including the varieties found in man) the *fl. fibularis* forms at least half of the hallux tendon (except in Schulze's example of *Pithecia*, in which three-fourths of the hallux tendon was from the *quadratus plantae*, the remaining one-fourth from the *fl. tibialis;* and in his *Callithrix* in which the great toe was supplied by the *quadratus plantae* alone), whereas in No. 47 the *fl. tibialis* contributes over three-quarters of the fibres. This predominance of the *fl. tibialis* in the formation of the hallucal tendon occurs also, according to Dobson (1883), in certain Marsupials and Chiroptera, and in the Insectivore *Centetes ecaudatus*, which he regards as exhibiting the essentially primitive mammalian arrangement of the long flexor tendons. In these animals the *fl. tibialis* predominates in the formation of the tendon to the hallux, sometimes to the virtual exclusion of the *fl. fibularis*.

Participation of the fibular flexor in the tendon for the fifth toe is also unusual among higher Primates. The condition found in No. 47, in which the minimus is supplied only by the fibular flexor, seems to have no parallel among the known great apes; it occurred, however, in Hepburn's gibbon and Meckel's spider monkey (*Ateles*). Glaesmer finds that toe V is supplied only by the fibular flexor in a number of mammals: namely, the Monotremes, some Marsupials, a number of Edentates, and certain Insectivores. I believe that it would be unfair, on the basis of the single known specimen, to state that the highland gorilla differs from the lowland species in the arrangement of the long flexor tendons. The distribution of the tendons in No. 47 should rather be regarded as a variation of very primitive type. These primitive characters in the long flexor tendons of No. 47 are: a) their high degree of fusion, recalling the condition found in prosimians and in other orders of mammals; b) the predominant part played by the *fl. tibialis* in the formation of the hallucal tendon, an arrangement not normally encountered among the Primates, but occurring in some other mammals; and c) the derivation of the outermost tendon from the *fl. fibularis* alone, also an essentially non-Primate condition. For a further discussion of the long flexor muscles in Primates the reader is referred to Keith (1894, 1929).

In conclusion, it must be mentioned that the long flexor tendons of Primates are not entirely formed by fibres from the *fls. fibularis et tibialis* alone. The *quadratus plantae* may contribute considerable tendinous elements to certain of the long flexor tendons. This phenomenon will be discussed in the following section.

M. quadratus plantae (fig. 23). This muscle, the *flexor accessorius* or *caro quadrata* of the older anatomists, is not always present in the gorilla. It has been found by Hepburn, Huxley, Macalister, and Owen. In the specimen of Huxley it is described as well-developed, in those of Hepburn and Macalister it was feeble and small, while Owen merely notes its presence. Bischoff, Chapman, Deniker (2 animals), Pira and Sommer definitely state that the quadratus was missing. Hartmann does not commit himself as to its absence or presence. The muscle is neither mentioned in the text nor figured in the plates of Duvernoy. I have found not a trace of this structure in a lowland gorilla (No. 1105), nor in the highland example (No. 47). If we regard it as absent in the animals of Duvernoy and Hartmann—and I have no hesitation on this score—we find the *quadratus plantae*

present in only 30.8 per cent (4 out of 13) of the lowland gorillas; add to this list No. 47, and it occurs in only 28.6 per cent (4 out of 14) of all gorillas. According to the figures collected by Keith (1899), it was present in six out of ten gorillas (60 per cent). As to its occurrence in other anthropoid apes (after Kohlbrugge): present in seven out of fourteen chimpanzees (50 per cent); present in six out of thirteen orangs (46.2 per cent); and always absent in the gibbons (8 examples). Keith (1899) states that it was present in six out of eleven chimpanzees (54.5 per cent). This muscle is but rarely completely absent in man (Le Double).

The *quadratus plantae* is always found in Old World monkeys (Bischoff, 1870; Glaesmer; Kohlbrugge; Ribbing; Straus). It is also normally present in the New World forms (Ribbing did not, however, find it in *Cebus fatuellus*). This muscle is always lacking in lemurs (i.e., lacking in all those examined by Glaesmer, Murie and Mivart, Ribbing, Weidenreich, Zuckerkandl and Straus). Burmeister, Duckworth, Ribbing and Woollard did not find it in *Tarsius*. I found no *quadratus plantae* in the orang, *Hylobates pileatus* and *Galago*. It was present in both the chimpanzee and *Pygathrix germaini*. In these it was a single-headed muscle arising from the outer surface of the calcaneus. According to Glaesmer, Leche and Ribbing, it may be absent in some other mammals, e.g., some Insectivores, most Chiroptera, Ungulates, some Edentates, Carnivores and Rodents, and most Marsupials.

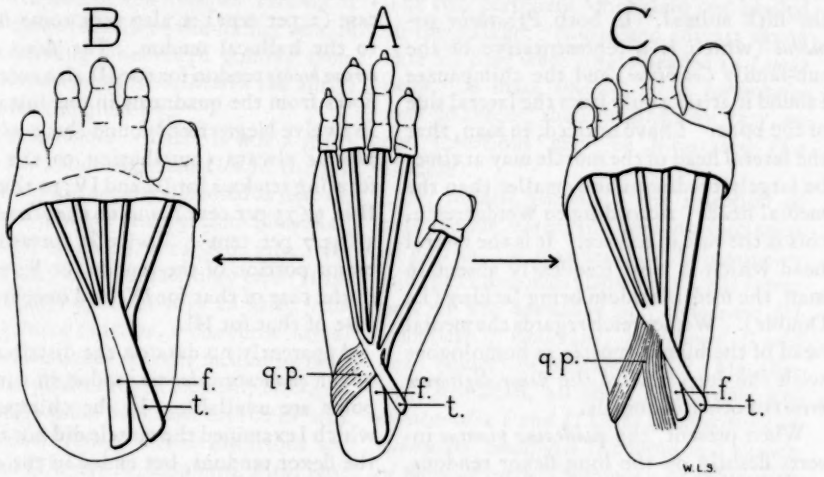


FIG. 23. TWO DIRECTIONS OF EVOLUTION OF THE QUADRATUS PLANTAE MUSCLE IN PRIMATES

A. Primitive type, consisting of a single lateral head, as in both New and Old World monkeys and some orang-utans, chimpanzees and gorillas. B. Complete absence, as in all prosimians, rarely in monkeys (one case), all gibbons, some orangs, chimpanzees and gorillas, and rarely in man. C. two-headed type, as in man (large majority) and rarely in orang (one case). *q. p.* = quadratus plantae; *f.* = flexor fibularis tendon; *t.* = flexor tibialis tendon.

In all Primates except man the muscle consists of but a single head (Kohlbrugge), which usually arises from the lateral side

of the calcaneus. However, Hafferl (1929) has recently described a two-headed *quadratus plantae* in an orang-utan.

Kohlbrugge notes that the origin is sometimes, on the other hand, from the medial instead of the lateral side of the calcaneus, e.g., in some chimpanzees and constantly in his *Colobinae* (*Semnopithèci*). The muscle arose from the medial side in four of the chimpanzees studied by Fick (1925); it was absent in the fifth animal. In both *Pygathrix germaini* (which is a representative of the sub-family *Colobinae*) and the chimpanzee I found it arising only from the lateral side of the bone. I have noticed, in man, that the lateral head of the muscle may at times be largely tendinous and smaller than the medial head. According to Weidenreich, this is the rule in fetuses. It is the lateral head which is most frequently absent in man, the medial seldom being lacking (Le Double). Weidenreich regards the medial head of the human muscle as homologous with the deep head of the *flexor digitorum brevis* of other mammals.

When present, the *quadratus plantae* inserts fleshily on the long flexor tendons, and in addition contributes to the formation of certain of these tendons through the medium of tendinous elements. In man, these contributions are given, as a rule, according to Schulze, to the long flexor tendons for toes II, III and IV, and also in 40 per cent of all cases to that for V. Customarily, in his specimens, most of the quadratus tendon went to those for III and IV, and a smaller portion to II; when part went to V, this was usually small. In one foot (1 per cent) Schulze saw a not insignificant tendon bundle of the quadratus going to the tendon for the hallux. The perforating tendon for II usually derived one-fifth of its fibres from the quadratus; that for III one-third; that for IV one-third; and that for V received varying amounts up to as much as one-third of its volume. Turner found essentially the same arrangement of the *quadratus plantae* in his series. The muscle usually contributed to the perforating tendons of toes II, III and IV, and often to that of V. He found that in a few cases the long flexor tendon for V was almost entirely formed by the quadratus, and in one foot (2 per cent) this tendon was apparently entirely thus constituted. In one case (2 per cent) it also sent some fibers to the hallucal tendon. The *flexor digitorum brevis* tendon for toe III also received fibres from the quadratus in one instance. In twelve Negro feet I found the *quadratus plantae* always contributing to the perforating tendons for III and IV; to that for II in 9 (75 per cent); and to that for V in 5 (41.7 per cent). Twice it formed the major portion of the tendon for V; twice in the case of that for IV; and once in the case of that for III.

Apparently no data on the distribution of the *quadratus plantae* tendon in anthropoids are available. In the chimpanzee which I examined the muscle did not reach the flexor tendons, but ended in the adjacent ligamentous tissue. Humphry (1867) found the same condition in one of his chimpanzees. Among Old World monkeys Schulze found that the tendinous portion of the *quadratus plantae* was distributed to the long flexor tendons for toes II, IV and V in *Papio* (*Cynocephalus*) *porcarius* (2 specimens), or only to those for II and V in *Erythrocebus patas* (*Cercopithecus ruber*) and 2 examples of *Lasiopyga* sp.? (*Cercopithecus* sp.?). Pagenstecher found that the *quadratus plantae* joined the *flexor fibularis* tendons to toes I, III and IV in *Papio leucophaeus* (*Mandrilla leucophaea*). In *Pygathrix germaini* most of the fibres go to the tendon for toe II, a lesser number to that for V, and the smallest portion to the tendon for the hallux through the *fl.*

tibialis element to that toe (Straus). In New World monkeys Schulze noted that the quadratus tendon was divided to toes IV and V in *Ateles*, to II and V in *Saimiri sciureus* (*Chrysothrix sciurea*), to V alone in *Cebus capucinus*, and to I only in *Pithecia chiropotes* (*rufimana*) and *Callithrix jacchus* (*Jacchus vulgaris*). Whereas in Schulze's Old World forms the *quadratus plantae* always contributed only a minor portion to the respective tendons, in *Pithecia* it formed three-fourths of the hallux tendon (the remaining one-fourth coming from the *fl. tibialis*) and in *Callithrix* the entire tendon for the great toe.

Mm. lumbricales. There is not a great deal to say about these muscles in the gorilla. They are usually disposed as in man, four nearly always being present (Bischoff, Duvernoy, Hepburn, Pira, No. 1105, No. 47), but they may number only two (Huxley). They appear always to arise from the long flexor tendons. The three lateral arise by two heads and the medial by one, as in man (Duvernoy, Hepburn, No. 47), but in one animal only that for toe IV was two-headed (Pira). Their insertions are as in man (Duvernoy, Hepburn, Pira, No. 47). Deniker and Sommer state that the *lumbricales* did not differ from those of the human foot. They are powerful, well-developed muscles in the gorilla (Bischoff, Chapman, Hartmann, Owen, No. 47).

The *lumbricales* usually are four in number in the other anthropoids and in monkeys. In prosimians they likewise customarily number four, but there may be only three in *Nycticebus coucang* (*tardigradus*) (Murie and Mivart), *Perodicticus*, and some *Indrisinae* (Ribbing), or as many as seven in *Loris* (*Stenops*) *tardigradus* (Glaesmer) and *Tarsius* (Allen), and their insertions are sometimes more complex than in other Primates. Burmeister, Ribbing and Woollard each describe four for *Tarsius*. Single-headed *lumbricales* are not very uncommon in the orang (usually the case for toes II, IV and V), and also occasionally occur in the gibbons and *Colobinae* (Kohlbrugge). In my orang all except that for digit III arose by only single heads from the tibial sides of the respective long flexor tendons. The two medial muscles were single-headed in my chimpanzee. In the *Pygathrix germaini* those for II and V arose by single heads. The two peripheral ones were one-headed in the galago. Murie and Mivart found that all four were single-headed in *Lemur catta*. In man, one or more *lumbricales* may be absent; their origins may vary, or the insertions may be bifurcated (Le Double).

M. tibialis posterior. The insertion of this muscle varies in different specimens of gorilla. It may be into the *naviculare* and the cuneiforms (Duvernoy), the lower part of the *naviculare* and *cuneiforme III* (Hepburn), *naviculare*, *cuneiforme I* and head (base?) of *metatarsale III* (Macalister), *naviculare*, all three cuneiforms and *metatarsalia I* and *II* (Pira), tuberosity of *naviculare*, *cuneiforme I*, cuboid and sheath of *peroneus longus* (Sommer), or tuberosity of *naviculare*, the cuneiforms, *sustentaculum tali* and sheath of *peroneus longus* (No. 47). Keith (1929) states that the *tibialis posterior* in the gorilla ends primarily in the bases of *metatarsalia II*, *III* and *IV* and in the ligamentous tissues at their bases, while the attachment to the *naviculare* and the inner side of the foot is only partial and secondary. (In the highland gorilla (No. 47), however, the insertion on the tuberosity of the *naviculare* is most marked, and in Sommer's gorilla this attachment was the primary one.) Furthermore, he states that a similar mode of insertion is found in all Primates except man.

The muscle inserts in man on the tuberosity of the *naviculare*, *sustentaculum tali*,

the three cuneiforms, cuboid, and the bases of the three middle metatarsals, and it is somewhat connected with the sheath of the *peroneus longus* tendon (Bryce). It has been observed to be missing in man, or it may be doubled, forming a so-called "*tibialis secundus*" (Le Double).

For a detailed account of the *tibialis posterior* in other Primates, the reader is referred to Forster (1922). In the chimpanzee the tendon inserts chiefly on the *naviculare* tuberosity, but there is likewise a strong attachment to the two outer cuneiforms (Forster, Hepburn, Straus). In the orang the insertion is on the *naviculare* tuberosity, the three cuneiforms and sheath of *peroneus longus* (Straus), or only on the *naviculare* and peroneal sheath (Hepburn). Forster found that the *naviculare* insertion in his orang was not as strong as the attachment to the cuneiforms. The attachments of the tendon vary among the gibbons. In *Hylobates pileatus* the muscle inserts by a strong tendon on the under side of the *naviculare*, and also sends a tendinous sheet to the two outer cuneiforms, cuboid, and the bases of the three middle metatarsals (Straus); in *H. lar* part of the tendon inserts on the *naviculare*, the rest on the calcaneus, cuboid, and the two outer cuneiforms (Forster); in *H. agilis* the insertion is on the *naviculare* tuberosity and the two outer cuneiforms (Kohlbrugge); and in *Symphalangus* (*Hylobates*) *syndactylus* the tendon goes to the *naviculare* tuberosity and *metatarsale III* (Kohlbrugge). Hepburn found the insertion to be on the *naviculare*, sheath of *peroneus longus*, and plantar ligaments in his gibbon.

The insertion in *Pygathrix germaini* is partly on the *naviculare* tuberosity, and chiefly on *cuneiformia II* and *III* and the *peroneus longus* sheath (Straus). In both Old and New World monkeys (see Forster, Kohlbrugge, Ribbing, Rosenfeld) the insertion is usually on the *naviculare* and the two outer cuneiforms, but the former attachment may be relatively slight or altogether absent. The tendon may reach the three middle metatarsals, it may end on the *naviculare*, or it may insert on the *talus*. As a rule, the *naviculare* attachment is secondary, as Keith (1929) has pointed out, and it is not usually as strong in monkeys and anthropoid apes as it is in man.

In *Galago* the tendon ends on the *naviculare* (Straus). This is the rule in most prosimians (Allen, Burmeister, Forster, Murie and Mivart, Ribbing, Woollard), but the tendon sometimes reaches one or more cuneiforms (Forster, Glaesmer, Milne Edwards and Grandidier, Murie and Mivart, Ribbing, Rosenfeld), and also the bases of the second and third metatarsals (Rosenfeld).

M. flexor hallucis brevis. Two distinct heads are usually present in gorillas (Bischoff, Deniker, Duvernoy, Hartmann, Hepburn, No. 1105). The fibular head may, however, be missing (Pira, Sommer), or it may be united with the oblique adductor (No. 47). Perhaps the fibular head was actually not absent in the animals of Pira and Sommer, but may have been fused with the adductor as in No. 47. The heads usually have distinct origins. The tibial head may arise from the *naviculare* and *cuneiforme I* (Duvernoy, Pira), or from these two bones and the sheath of the *peroneus longus* tendon in addition (No. 47), or from the peroneal sheath alone (No. 1105), or from the *cuneiforme III*, peroneal sheath and from the ligamentous structures between this and the tendon of the *tibialis posterior* (Hepburn), or from the end tendon of the *tibialis posterior* (Sommer). The fibular head arises from the outer border of the hallucal metatarsal bone (Bischoff, Duvernoy, Hepburn, No. 1105), or from the first and second cuneiforms and the *peroneus longus*

sheath (No. 47). What is clearly the fibular head is described together with the plantar interossei by Duvernoy. There is nothing of particular interest about the insertions—the tibial head usually inserts with the abductor of the great toe, the fibular with the adductor. Part of the tibial head may insert on the inner border of the shaft of the first metatarsal, forming an *opponens hallucis* (Hepburn, No. 47). The accessory short flexor of the hallux found by Deniker in his gorilla fetus has already been discussed with the *flexor digitorum brevis*.

The *flexor hallucis brevis* has, in general, a similar structure in other Primates. In man the two heads are products of a single belly of origin. It is often inseparably fused with the adductor (Bryce). The tibial head is steadily larger than the outer (Kohlbrugge), which may be fused with the adductor (orang, described by Ruge, 1878b).

There are usually two heads present in monkeys (Kohlbrugge; Ruge, 1878b). Bischoff (1870) found the *flexor hallucis brevis* composed of two heads in all of the Old and New World monkeys which he studied.

Among prosimians, only the tibial head is present in *Lemur* (Cunningham), only the fibular in *Galago crassicaudatus*, *G. alleni* and *G. garnetti* (Murie and Mivart). Apparently these last-named investigators found both heads in *Lemur catta*. Two heads are described by Woollard in *Tarsius*, but only one (the fibular) by Burmeister.

M. opponens hallucis. This muscle is a derivative of the tibial head of the *flexor hallucis brevis*. It was present merely as an attachment of some of the fibres of the tibial head of the *flexor brevis* to the distal half of the inner border of the shaft of *metatarsale I* in Hepburn's gorilla. A somewhat similar arrangement occurs in No. 47, but the insertion is much less extensive than in Hepburn's animal; in fact, in my specimen the muscle is exceedingly rudimentary, and probably was almost, if not entirely, functionless. Hartmann speaks of an *opponens hallucis* in his gorilla as if it were a separate muscle, and Macalister does likewise. The latter states that it "inserted into the metacarpal bone." I am not quite certain that the muscles described by Hartmann and Macalister under the name of opponens of the great toe can really be regarded as such, especially since details of their insertions are not given. The muscle which Macalister calls the opponens may possibly be the fibular head of the *flexor hallucis brevis*. A true *opponens hallucis* must so insert on *metatarsale I* that its contraction produces opposing action of that toe. The fibres of the *adductor hallucis* which frequently insert in anthropoids on the outer border of the first metatarsal have been regarded by some writers as constituting an *opponens hallucis* ("*adductor opponens*"), but this clearly is a misnomer. Opposition of the hallux by action of such an adductor is impossible. Bischoff, Deniker, Pira and Sommer found no *opponens hallucis*, and there was none in No. 1105. Chapman, Duvernoy, Huxley and Owen make no mention of such a muscle. There can be little doubt that a well-developed *opponens hallucis* is, at best, very rare in the gorilla. I hesitate to estimate the percentage frequency of its occurrence with the unsatisfactory data now at hand.

The opponens is an almost constant occurrence in the orang, in which it may be a separate muscle, arising from the tarsal bones and inserting on the lateral edge and under surface of the first metatarsal, as in Bischoff's (1870) animal, or else still attached to the *flexor hallucis brevis*, and inserting in the inner border of the hallucal metatarsal, as in the orangs of Hepburn, Primrose and Straus. The opponens of

the great toe is extremely rare in other Primates. It may sometimes occur as a separate structure in man (Le Double). Hartmann found "a slightly developed opponens" in a gibbon. I can find no reference to it in chimpanzees. It occurs only occasionally in Old World monkeys, e.g., in the *Pithecus* (*Macacus*) studied by Bischoff, in which it was a separate muscle arising from the tarsus, and in the *Papio cynocephalus* (*Cynocephalus babuin*) of Michaelis, where it originated from the first cuneiform. Kohlbrugge notes its absence in his *Colobinae*. Apparently this muscle does not occur in either New World monkeys or prosimians.

M. adductor hallucis. This muscle is the innermost member of the group of contrahentes (adductors) muscles. In gorillas it is usually divided, somewhat as in man, into two distinct heads, oblique and transverse (Bischoff, Chapman, Duvernoy, Hepburn, Huxley, Macalister, Owen, No. 47), but it may be a single fan-shaped mass (Pira, Sommer). In Deniker's fetus it was divided into five distinct fascicles laid out fanwise. A somewhat similar arrangement was found in No. 1105, in which the muscle is fan-shaped but divided into three parts. In cases where actual division into oblique and transverse heads occurs, the oblique head arises from the bases and proximal portions of *metatarsalia II* and *III* (Duvernoy), or from the proximal portion of an aponeurotic raphe extending along *metatarsale III* (Hepburn), or from the bases of *metatarsalia II* and *III*, sheath of *peroneus longus* tendon, and fascia over the intervening interosseous muscles (No. 47). The transverse head may take origin from (heads of?) *metatarsalia II–V* (Bischoff). It may arise from the heads of *metatarsalia II–IV* (Huxley) or from the heads of *metatarsalia III* and *IV* (Macalister). Duvernoy found it arising from the ends of *metatarsalia II–IV* and an aponeurosis which ran for the length of *metatarsale II*. It took origin from the heads of *metatarsalia II* and *III* and the distal portion of an aponeurotic raphe extending along *metatarsale III* in Hepburn's animal. In No. 47 it arose from the distal parts of the shafts and proximal parts of the heads of *metatarsalia II–IV*, from the associated joint-capsules and transverse metatarsal ligaments, the intervening interosseous fascia, and the deep portion of the *aponeurosis fibularis* (No. 47). Hepburn does not give a detailed description of the origins of the two heads, but his figures make the conditions quite clear. In Pira's animal the adductor arose from *metatarsalia II–IV*, in Sommer's from the bases of *metatarsalia II* and *III* and from a tendinous arch which ran from the base to the head of *metatarsale III*. Deniker's fetal gorilla had the adductor split into five fascicles, which took origin from metatarso-phalangeal joints II, III and IV, the middle of *metatarsale IV*, and the proximal part of *metatarsale III*. In No. 1105 the situation was as follows: the proximal portion of the muscle arose from the proximal part of a tendinous raphe extending from the *peroneus longus* sheath to the metatarso-phalangeal joints and from the middle of *metatarsale II* to the middle of *metatarsale IV*, the middle portion from the intermediate part of that same raphe, and the distal portion from the inner border of the raphe and proximal parts of the heads of *metatarsalia II* and *III*. The muscle usually has the same general insertion, both heads (if two are present, or if not, the single head) attaching to the outer side of the basal phalanx of the hallux. In some cases the fibres may extend to the distal phalanx (Duvernoy) or into the distal portion of the outer side of the first metatarsal (Duvernoy, Hepburn, Pira, No. 1105, No. 47) to form the so-called *adductor opponens*, which is a misnomer.

In such metatarsal insertions the fibres are chiefly or entirely from the distal portion of the muscle (transverse head). There also were some adductor fibres attached to the first metatarso-phalangeal joint in Nos. 1105 and 47.

Since the *adductor hallucis* will be discussed in a later publication dealing with the deep muscles of Primate feet, I shall not enter into any further details here. It will be sufficient to note that this muscle may be a single mass or else be divided into two heads in the other anthropoids, monkeys and prosimians.

In man two distinct heads are present, the transverse being weaker than it generally is in other Primates, and it usually arises from the three lateral metatarsals. Leboucq (1895) describes an anomalous fascicle, in three out of sixty European feet, which he believes to represent the middle portion of the *adductor hallucis* of other Primates. In early stages of human development the adductor is not yet divided into distinct oblique and transverse heads. The definitive adult arrangement is arrived at by a migration of the eventual transverse head from the lateral side of the oblique head to the outer border of the foot, and distally to the heads and joint-capsules of *metatarsalia III–V* (Ruge, 1878c). The transverse head may retain an embryonic position, or it may be entirely absent (Ruge, 1878c; Le Double).

Mm. contrahentes II, IV, V (fig. 24). These muscles, members of the same layer as the *adductor hallucis*, are normally absent in gorillas. They were found completely absent by Bischoff, Deniker, Hartmann, Hepburn, Pira, and Sommer. I found no trace in Nos. 1105 and 47 (the aponeurotic sheet covering the interossei in No. 47 might be regarded, as previously stated, as constituting vestiges of the distal portions of the lateral section of this layer). Duvernoy does not speak of them, nor are they figured in his excellent plates. An

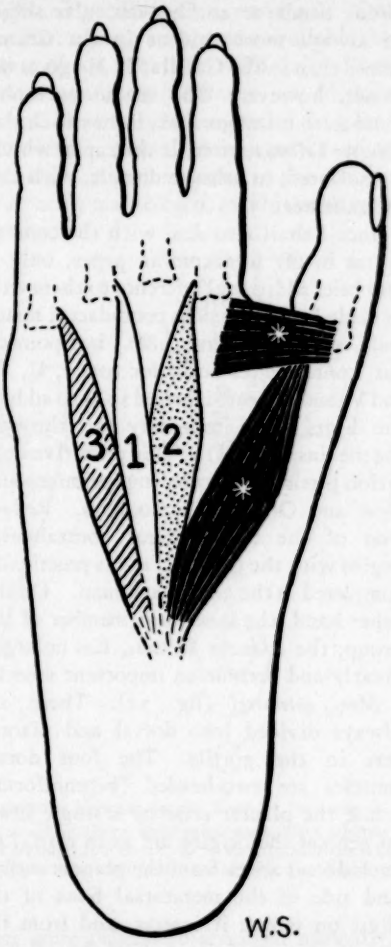


FIG. 24. PHYLOGENETIC ORDER OF DISAPPEARANCE OF THE CONTRAHENTES MUSCLES OF THE FOOT IN PRIMATES

The muscles are numbered in the order of their disappearance. *1* = contrahens digiti IV; *2* = contrahens digiti II; *3* = contrahens digiti V; * = contrahens digiti I (adductor hallucis), which is present in all Primates. Based on data collected by the author.

adductor of the fifth toe was present in Macalister's gorilla. This is in all likeli-

hood a *contrahens V*. Keith (1899) states that "the contrahentes muscles, either as fibrous bands or as fibro-muscular slips, are always more evident in the Chimpanzee than in the Gorilla." He gives no details, however. The tendinous raphe found in so many gorillas, from which the *adductor hallucis* arises, is the raphe which is associated, in other mammals, with the contrahentes.

Since I shall also deal with the contrahentes in my forthcoming paper, only a very brief additional reference to them will be made here. In most pentadactyl mammals, as Cunningham (1882) has pointed out, contrahentes occur for toes I, II, IV and V, and they are inserted so as to adduct the digits to an imaginary axis through the medius (toe III). This primitive condition persists, as a rule, in prosimians and New and Old World monkeys. Reduction of the three lateral contrahentes begins with the gibbons, and is practically completed in the gorilla and man. On the other hand, the innermost member of the group, the *adductor hallucis*, has enlarged greatly and become an important muscle.

Mm. interossei (fig. 25). These are always divided into dorsal and plantar sets in the gorilla. The four dorsal muscles are two-headed (bipenniform), while the plantar arise by a single head. In general the origins are as in man, i.e., each dorsal arises from the plantar surface and side of the metatarsal bone of the digit on which it inserts, and from the dorsal portion of the shaft of the adjacent metatarsal; each plantar arises from the plantar surface and side of the metatarsal of the digit of insertion. There may be a partial origin from the *peroneus longus* sheath, as in No. 47. Insertion of both dorsal and plantar are into the bases of the basal phalanges and the extensor aponeuroses of the toes. The second head of the first dorsal interosseus may arise from *metatarsale I* (Hepburn), or from the first cuneiform (Nos. 5 and 47). *Dorsal interosseus II* may arise anomalously by only a single head from *metatarsale II* (Deniker), while *plantar interosseus I* may have two heads of origin, from the adjacent *metatarsalia* (Hepburn), and similarly two heads may be present for *plantar interosseus II* (Deniker). Bischoff's gorilla exhibited a strange arrangement of the interosseous muscles in the right foot, which had two dorsals for the second toe and likewise two dorsals for the fourth toe, while the third digit possessed two plantars; the left foot had the usual gorilline arrangement, with two dorsals for the second toe, one for the third, and one for the fourth. In the gorilla both sets of interossei project markedly into the sole.

By far the most interesting fact in connection with these muscles pertains to their arrangement around the digits. In most gorillas the interossei are oriented so as to ab- and adduct from and to an axis passing through the second toe (Bischoff: left foot, Deniker, Hepburn, Pira, Sommer, Symington, No. 7, No. 47), but in some examples the axis is through the middle digit (Duvernoy, Macalister, No. 5). Thus, in 72.7 per cent (8 out of 11) of gorillas the interosseal axis is through toe II. Keith (1899) in reporting from the literature, states that "in 3 out of 7 Gorillas, the second digit, as is the case in Man, received the insertion of the first and second dorsal interossei muscles." The interossei of Primates will be considered in detail in my paper on the deep foot musculature, and a preliminary report on these muscles has already been published (Straus, 1929a). It is merely necessary again to state here that gorilla and man are the only Primates in which the pedal interossei are usually arranged around the second toe. The human condition may occur as a variation in the other

anthropoids, but apparently in both Old and New World monkeys the axis is always through the third digit, as it is in most pentadactyl mammals. The prosimians show their own type of specialization by often having the axis through the fourth toe, which is usually the longest in these animals. It is interesting to note that both specimens of highland gorilla (Nos. 7 and 47) have the human arrangement, whereas the lowland gorilla exhibits the usual Primate condition in 33 per cent of the known cases (3 out of 9). In order to decide whether this is really a specific difference, more specimens, especially of the highland form, must be obtained. At any rate, such a difference could only be an average one.

The slip of muscle which arises from the distal portion of the plantar surface of the shaft of *metatarsale III* and splits to insert on the adjacent sides of the second and third toes I have found only in the two highland gorillas (Nos. 7 and 47). Only one foot of each animal was available (the left of No. 7, the right of No. 47). I have not thus far encountered an identical muscle in any other animal. I recently saw what appeared to be a partly, if not entirely, similar condition in the left foot of an adult male Negro, in which the interossei were otherwise arranged normally. From the plantar surface of the second dorsal interosseus (for the fibular side of the second toe) there arose distally a fleshy slip about 3 mm. in diameter which was inserted into the tibial side of the metatarso-phalangeal joint-capsule of the third toe. There was no bifurcation to the second toe joint-capsule as in the highland gorillas. The condition described by Ochiltree (1913) in the right foot of an

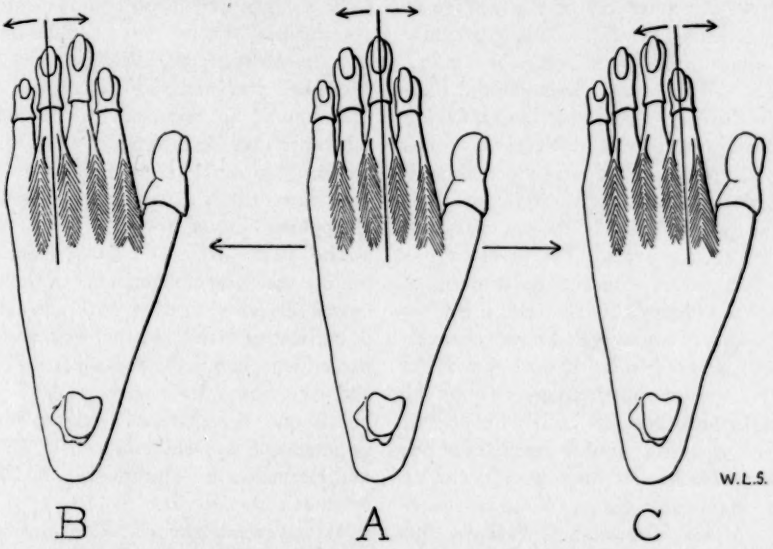


FIG. 25. TWO DIRECTIONS OF EVOLUTION OF THE INTEROSSEOUS MUSCLES OF THE FOOT IN PRIMATES

A. Primitive condition, with axis through third toe, as in all monkeys, some prosimians, most gibbons, orang-utans and chimpanzees, and a few gorillas. B. Axis through fourth toe, as in some prosimians. C. Axis through second toe, as in a few gibbons, orangs and chimpanzees, most gorillas, and all men. Based on data collected by the author.

adult male human, seems to be analogous, if not homologous, with the condition in the *Gorilla beringei*. In reference to the *adductor hallucis*, Ochiltree states that "this muscle possessed an accessory slip which arose from the lateral border of the muscle and was inserted into the adjacent sides of the proximal phalanges of the second and third digits." The muscle-slip in this foot seems, from its association with the adductor (obliquus?) to be the vestige of the contrahens of the second toe (only very occasionally occurring in man), whereas in the two *G. beringei* (and likewise in the Negro) the muscle in question is almost certainly a derivative of the interosseous layer. If we cannot homologize these muscle-slips, at least their general insertions in the two gorillas and the men are the same. The literature, as far as I am aware, contains no accounts of a condition identical with that in my gorillas. It is of course well-known that certain of the *lumbricales* of both hand and foot in man may bifurcate and insert on the two adjacent digits (cf. Le Double on this point). A similar double insertion of one or more *lumbricales* may also occur in other mammals: viz., *Phascogale* (Ribbing), *Manis* (Glaesmer). Perhaps this condition is analogous to that occurring in the two highland gorillas. Eisler (1895b) describes, in the amphibian *Menopoma*, muscles which arise from the distal ends of each metatarsal bone and insert on the basal phalanges; he has seen such a muscle well-developed in a gorilla (certainly a *G. gorilla*, judging from the date of this publication) and also indications of it in man. Possibly this muscle is homologous to that which I have found in my gorillas.

M. flexor digiti V brevis. This muscle arises in the gorilla essentially as in man, from *metatarsale V* and the sheath of the *peroneus longus* (Hepburn, Pira, No. 47). An additional superficial layer such as I found in No. 47, from the *peroneus longus* sheath, cuboid, and bases of *metatarsalia IV* and *V*, is not mentioned by any other workers (Hepburn, however, notes that it had an additional origin from the base of *metatarsale IV* in his orang). The insertion is on the outer side of the basal phalanx of the little toe (Duvernoy, Hepburn, Pira, No. 47), and in No. 47 there appears to be a slight expansion into the extensor aponeurosis of that toe in addition. It was united with the *abductor digiti V* in Bischoff's specimen, and it inserted with that muscle in Sommer's. The muscle-substance may be pierced by the abductor tendon (No. 47). It is difficult to separate from the third plantar interosseus (Hepburn, No. 47).

The *flexor digiti V brevis*, which is plainly the outermost member of the interosseus series, is a rather constant element of the feet of man and other Primates. In these forms it has the same general origin and insertion. It is never really absent, but it may be entirely converted into an opponens, as in Deniker's gorilla, Ribbing and Hermansson's chimpanzee, and Zuckerkandl's *Daubentonia*.

M. opponens digiti V. This muscle is a derivative of the *flexor digiti V brevis*. In the gorilla it is sometimes present as a portion of the latter (Bischoff, Hepburn, Pira), but it can be a distinct muscle (Deniker). It may be lacking (Hartmann, No. 47). Chapman, Duvernoy, and Macalister, all of whom note the presence of a *flexor digiti V brevis*, do not mention an opponens. In the animals of Bischoff and Pira it was merely represented by certain fibres of the *fl. dig. V brevis* which inserted into the outer border of *metatarsale V*, while in Deniker's fetus a true *fl. dig. V brevis* was absent, the entire muscle having been converted into an opponens. Hepburn found the opponens portion to be

better-developed than the flexor element, the two muscles, however, arising in common. The presence of an *opponens digiti V* has been noted by Sommer, who states that it was united with the flexor at its origin. Yet the muscle which he describes certainly cannot have been a true opponens, for he states that its insertion was on the medial side of the base of the basal phalanx of the fifth toe.

The opponens of the little toe commonly occurs in all groups of Primates. It is found in a majority of men, but merely as a part of the *fl. dig. V brevis*, yet it may occasionally be a separate and independent slip (Bryce). It has also been found in chimpanzee and gibbon (Kohlbrugge), in chimpanzee (Ribbing and Hermansson), in orang and macaque (Le Double), and in a number of prosimians (in *Daubentonia madagascariensis*, *Lemur variegatus* and *Galago crassicaudatus* by Zuckerkandl, and in *Lemur catta* by Murie and Mivart). As I have mentioned, the entire *flexor digiti V brevis* may at times be converted into an opponens.

M. extensor hallucis longus. There is little to say about this muscle. It inserts regularly on the terminal phalanx of the great toe (Hepburn, Owen, Pira, No. 47). Plate IX of Duvernoy shows a similar attachment. Sommer states that the tendon goes into the dorsal aponeurosis of the first toe.

In man and the other Primates the end tendon has a like termination on the terminal phalanx of the hallux (Bischoff, 1870; Murie and Mivart; Zuckerkandl).

Ribbing's researches indicate that the development of this muscle in mammals is roughly proportional to the development of the hallux. In some forms he found it inserting in the second toe. Le Double has listed the types of variation in man; it may insert on both phalanges of the hallux, and it may furnish supernumerary tendons of various sorts. Similar variations occur in other Primates (Kohlbrugge).

Bardeen states that the *extensor hallucis longus* is to be looked upon as an especially differentiated portion of the *extensor digitorum longus*. In the human embryo, he found its tendon at first fused with the *ext. digit. longus* tendon plate. But even at early stages the muscles may be distinguished from one another.

M. extensor digitorum longus. Customarily in the gorilla it divides into three tendons, the two lateral going respectively to toes *V* and *IV*, the medial dividing more distally into tendons for toes *III* and *II* (Deniker, Duvernoy, Owen, Pira, Rothschuh (quoted by Weidenreich), Sommer, No. 47). Hartmann, Hepburn and Macalister merely note that the muscle supplied the four lateral toes. In Ranke's gorilla tendons were given off for toes II–V. His figure of this muscle (Tafel I) shows two primary tendons, one of which supplies toe V, while the other splits into three distinct parts for digits IV, III and II. In Pira's gorilla there was a *junctura tendinum* between the tendons for III and IV.

The long extensor of the toes usually supplies all of the four lateral toes in man and the other Primates (Ranke, Beattie, Murie and Mivart, Zuckerkandl). Ranke has carefully studied the distributions of the tendons and their connections. His diagrams (Tafel I) show that union of two or more end-tendons is the rule. Whenever any such union occurs, the tendons for toes II and III are always involved and intimately united, a condition which is the rule in the gorilla. In man I have encountered all degrees of separation of these tendons. There are not infrequently only three, as in the gorilla, the innermost later splitting into elements for the second and third toes. This later fusion of the

two most medial tendons is usually, though not always, an accompaniment of webbed toes (zygodactyly) in man (Straus, 1926). It does of course also occur in feet that are not webbed. Weidenreich also discusses this fusion of the tendons, and in great detail. Accessory tendons are not at all uncommon in man, and the muscle is subject to numerous types of variation. Sometimes it has connections with the metatarsal bones, e.g., in a gibbon dissected by Ranke the outermost tendon gave off a slip to the capitulum of *metatarsale IV*. There is no tendon for the second toe in *Lemur variegatus* (*varius*) and *Perodicticus potto* (Murie and Mivart). The second toe tendon was the smallest in No. 47, and Murie and Mivart found the same condition in *Nycticebus coucang* and *Loris tardigradus* (*gracilis*), as did Kohlbrugge in *Colobinae*. It may be missing in the latter and also in the orang (Kohlbrugge, Ranke). There thus seems to be a tendency to reduce or eliminate the supply to the second digit, at least in some forms.

The tendons of the long extensor, upon reaching the digits, continue as elements of the extensor aponeuroses. Willan has carefully isolated the elements of the extensor aponeuroses in man and certain species of baboons (*Papio cynocephalus* (*anubis*), *P. cynocephalus*, *P. sphinx*). Apparently Duvernoy was able to dissect the extensor aponeuroses in his gorilla in greater detail than I have been. Kohlbrugge gives some data on this point for *Hylobates* and *Colobinae*, and Hafferl does likewise for the chimpanzee.

M. peroneus tertius (fig. 26). This muscle is in reality a portion of the *extensor digitorum longus*. It is sometimes present in the gorilla, although so recent a text as Sonntag (1924) does not recognize its existence in this animal. In Rothschuh's (1888) gorilla the muscle was still fleshy distal to the cruciate ligament and was inserted by a broad tendon to the base of *metatarsale V*. Eisler (1895a) describes what may be regarded as a rudimentary *peroneus tertius* in the right foot of his gorilla; a small portion of the muscle-belly of the *extensor digitorum longus*, fibular to the belly for the fifth toe, passed beneath the cruciate ligament, giving rise to a thin tendon which ran to the middle of *metatarsale V* and could be traced to the capsule of the metatarso-phalangeal joint. The muscle was present as a very definite structure in the gorilla studied by Ranke (1897), who figures it in his Tafel I. In this illustration the muscle-mass of the long extensor of the toes gives rise to three tendons. The innermost of these splits into tendons for the second, third and fourth toes, the middle goes to the fifth toe, and the outermost is the *peroneus tertius*. Details of the insertion are, however, neither given nor pictured. What may be a rudimentary *peroneus tertius* is described by Sommer (1906). In his gorilla the lateral tendon of the long extensor to toe V split into two parts, one going to the dorsal aponeurosis of the fifth digit, while the other was attached on the lateral side of the base of *metatarsale V* and the membrane on the lateral side of this bone from base to head. Morton (1924) describes and figures the *peroneus tertius* in two gorillas. In a young male *Gorilla gorilla* it came from the muscle-mass of the long extensor, but arose from a definite belly; it inserted on the base of *metatarsale V* and was prolonged forward as a thin tendon to the outer side of toe V. This author also describes a *peroneus tertius* in the left foot of an adult female *Gorilla beringei*. This left foot is the mate to the foot which is the subject of the present paper (Comp. Anat. # 47, Amer. Mus. Nat. Hist.). In this left foot Morton found that the *peroneus tertius* tendon came from the common extensor muscle belly, and "the insertion was

located in the outer, upper aspect of the base of the fifth metatarsal bone. Just above this insertion ". . . . a thin, thread-like prolongation is carried forward to the digit, at a right angle to the tendon proper." I have already given a description of the *peroneus tertius* tendon in the right foot of this same animal. In the right foot, however, there is no thin tendon from the *peroneus tertius* to toe V. At the insertion it is pierced by a narrow tendon prolonged from *peroneus brevis* to the fifth digit (vestige of *peroneus digiti V*). The *peroneus tertius* was absent in the gorillas of Bischoff, Chapman, Deniker, Hartstructure as Sommer found is possibly a very rudimentary *peroneus tertius* in an early stage of its differentiation from the long extensor. Keith (1923) notes, in respect to the *extensor digitorum longus*, that "in the gorilla one notices occasionally a tendency for the outer fibres of the tendon going to the fifth or small toe to stray or migrate towards the outer border of the foot." The occurrence of the doubled fifth toe tendon in man, even in the presence of a well-defined *peroneus tertius*, might be regarded as an attempt to strengthen this muscle.

A *peroneus tertius*, in some form, occurs therefore in 33.3 per cent of gorillas (6 out

FIG. 26. PERONEUS TERTIUS MUSCLE IN CHIMPANZEE, GORILLA AND MAN, AND AN APPARENTLY HOMOLOGOUS MUSCLE (EXTENSOR TARSI) IN A MARMOSET (CALLITHRIX JACCHUS)

p. t. = peroneus tertius; *e. t.* = extensor tarsi. The chimpanzee foot is after Hecker, redrawn; the gorilla foot is after Rothschuh, reversed and redrawn from Forster (1916); and the marmoset foot is after Forster (1916), redrawn.

mann, Hepburn, Huxley, Macalister, Pira, and Symington, and likewise in No. 1105. Duvernoy neither mentions nor figures it, nor does Owen, so that one may rightly assume its absence in these animals. Pira claims, and with some justification, that the tendon which Sommer has described as that of a *peroneus tertius* is not actually such a structure. He points out that in man, even when a true *peroneus tertius* is present, the long extensor tendon for V may sometimes be doubled, the extra tendon going to the fifth metatarsal. I have myself seen this in the dissecting room and Morton describes and figures the same condition in his young lowland gorilla. But such a

of 18 animals), if we include the doubtful case of Sommer, or, if we regard Sommer's animal as really lacking this structure, in 27.8 per cent (5 out of 18 animals). In this computation, the two feet of No. 47 described by Morton and myself have of course been treated as a single specimen. In man the muscle varies a great deal in character, and it may be completely absent. It is present in 91.5 per cent of Europeans (Le Double); in 90 per cent (Krause, cited by Sommer). It may send a supernumerary tendon to the fifth toe (Testut, Le Double), as it does in Morton's gorillas.

A well-developed *peroneus tertius* has also been found by Hecker (1922) in a chim-

panzee, but this muscle does not occur in any other Primate. At least, I am not aware that a structure worthy of the name has yet been found. However, Forster (1916) describes a muscle (*M. extensor tarsi*) which inserted upon the outer side of the calcaneus in a specimen of *Callithrix* (*Hapale*) *jacchus*. This muscle, despite its unusual insertion, is most probably homologous to the *peroneus tertius* of man.

Apparently the presence of the *peroneus tertius* in man is not of paramount importance in the economy of the individual, for, as already stated, it is absent in about 10 per cent of cases. It is plainly a progressive structure, and is an attempt to further adapt the foot to the erect posture. Its great variability would suggest that it has, however, not yet attained its fullest development.

M. tibialis anterior. In all gorillas this muscle inserts by separate tendons on the inner aspect of the first cuneiform and on the inner side of the base of the hallucal metatarsal (Bischoff, Deniker, Duvernoy, Hepburn, Macalister, Owen, Pira, Ranke, Sommer, No. 1105, No. 47). In Duvernoy's animal the proximal tendon was also inserted on the *cuneiforme I-metatarsale I* joint-capsule, and in No. 47 this same tendon split to give off an accessory insertion into a large sesamoid. The distal tendon of Sommer's specimen was attached to the inner edge of the first metatarsal from base to head. There is considerable variability in the extent of the division of the two insertions. It may involve only the tendon, or the splitting may extend high up into the muscle-belly. In the gorilla dissected by Duvernoy the muscle very early divided into two bellies, so as to form two practically distinct muscles. The belly whose tendon was attached to the base of *metatarsale I* Duvernoy called the "long abductor of the great toe." In No. 47 there is of course no way of ascertaining the extent of the splitting, but the muscle-belly was certainly involved, for I found muscle fibres on the plantar surfaces of the tendons. Keith (1899) gives some collected data on the splitting of the tendon and muscle. He states that "of 7 Gorillas, only the tendon was divided in 5; the division extended deeply into the muscle in 2; in the Chimpanzee . . . . the muscle and tendon were divided in 16, the tendon only in 3." In the gorilla, the tendon to the first cuneiform is generally much stronger than that to the first metatarsal (Macalister, Pira, Sommer, No. 47). In Macalister's animal the tendon to the hallucal metatarsal was only one-fifth the size of that to the first cuneiform.

In the chimpanzee, as noted above, the division of the muscle is much more complete than in the gorilla. The insertion is limited to *cuneiforme I* and *metatarsale I* (Hepburn, Ranke, Straus). I found the cuneiform insertion to be much the stronger. In Bischoff's chimpanzee (1870) there was also a third insertion on the inner border of the foot.

In man the tendon is usually not divided until just previous to its insertion on the first cuneiform and first metatarsal, but the actual extent of splitting varies. The division may sometimes extend into the muscle-belly, and rarely the entire muscle may be divided in two (Le Double).

The insertion in the orang is *cuneiforme I* and first metatarsal (Hepburn, Ranke, Straus). In my animal the insertion on the cuneiform was the stronger. The extent of splitting varies considerably (Kohlbrugge). It may involve the whole muscle or the tendon alone, but it usually is not as extensive as in the chimpanzee (Sommer).

In the gibbons the muscle usually inserts on *cuneiforme I* and *metatarsale I*. This is the arrangement in *Hylobates leuciscus*, *H. agilis*, and *Symphalangus syndactylus* (Kohl-

brugge), *Hylobates* sp.? (Hepburn), *Hylobates I* (Ranke) and *Hylobates pileatus* (Straus). In Kohlbrugge's specimens there was an additional insertion on a small bone which lay between *cuneiforme I* and *metatarsale I*. The insertion may be limited to *cuneiforme I* (Bischoff's *Hylobates leuciscus*) or to *metatarsale I* (Ranke's *Hylobates II*). The tendon to the cuneiform was much the larger in my *H. pileatus*. Only the tendon may be split, as in *Symphalangus syndactylus* and *Hylobates leuciscus* (Kohlbrugge) and *Hylobates I* (Ranke), or the muscle-belly itself may be divided, as in Hepburn's gibbon.

Metatarsale I and *cuneiforme I* are the points of insertion in Old World monkeys (Kohlbrugge, Ranke, Pagenstecher, Straus). The cuneiform insertion was much the stronger in my *Pygathrix germaini*. Not only the tendon, but also the muscle-substance, at least in part, is always divided (Bischoff, Ranke, Ribbing, Straus). The muscle itself was split only distally in *Pygathrix cristata* (*Semnopithecus maurus*) (Kohlbrugge), and in *Pithecus irus* (*Macacus cynomolgus*), *Simia sylvanus*, *Lasiopyga griseoviridis* (*Cercopithecus sabaeus*), and *Papio cynocephalus* (*Cynocephalus babuin*) (Ribbing); the division of the muscle was complete in *Papio sphinx* (*Cynocephalus maimon*), *Lasiopyga* (*Cercopithecus*), and *Pithecus* (Bischoff), in *Nasalis larvatus* (*Semnopithecus nasicus*) (Kohlbrugge), and in *Papio* (*Cynocephalus*) *hamadryas*, *Pithecus* (*Macacus*) *nemestrinus*, *Erythrocebus patas* (*Cercopithecus ruber*), and *Lasiopyga* (*Cercopithecus*) sp.? (Ranke). In my *Pygathrix germaini* the upper portion of the leg was absent, so that I am unable to state the exact extent of the division. Not only the tendon, but also the portion of the muscle which was present, were entirely divided.

In New World monkeys the muscle usually inserts on both *cuneiforme I* and *metatarsale I*. It may, however, be limited to the first cuneiform, as Kohlbrugge found in *Leontocebus* (*Hapale*) *rosalia*. Both tendon and muscle are usually split, the latter entirely, so that two muscles seem to be present. This was the case in *Pithecia monacha* (*hirsuta*) and *Callithrix penicillata* (Bischoff), in *Cebus apella* and *Callithrix* (Ranke), in *Cebus fatuellus* and *Callithrix* (*Hapale*) *jacchus* (Ribbing). The tendon and only the distal part of the muscle-belly may be split, as in *Brachyteles* (*Ateles*) *arachnoides* (Ribbing) and *Alouatta ursina* (*Mycetes fuscus*) (Sirena). The tendon only may be split in *Callithrix* (*Hapale*) *jacchus* (Beattie).

Among prosimians the insertion may be on both the first cuneiform and first metatarsal, as in *Lemur variegatus*, *L. fulvus* (*xanthomystax*) and *L. nigrifrons* (Murie and Mivart), in *Lemur mongoz* (Ranke), in *Lemur mongoz* (Ribbing), and in *Daubentonia madagascariensis* and *Lemur variegatus* (Zuckerkandl). The insertion was only on the first cuneiform in *Tarsius* (Burmeister), in *Lemur catta* (Murie and Mivart), in *Lepidolemur* (*Lepilemur*) and *Tarsius* (Ribbing), in *Tarsius* (Woollard), in *Galago crassicaudatus* and *Loris tardigradus* (*Stenops gracilis*) (Zuckerkandl), in *Propithecus* (Milne Edwards and Grandidier), and in *Galago* (Straus). Both tendon and muscle are completely split in two whenever the insertion is on both cuneiform and metatarsal.

Kohlbrugge points out that in general among Primates the cuneiform insertion is the stronger, as I found in all of my specimens showing double insertions. The original insertion of the muscle in mammals, according to Ribbing, was on the first cuneiform. This would explain the relative weakness of the metatarsal attachment. Viewed in this light, the usual splitting of the muscle among Primates is a secondary phenomenon. Such

a splitting would procure an independence of the two components, an independence which might prove useful to a climbing animal.

Mm. extensores hallucis et digitorum breves. These are merely parts of a single muscle, and may be considered together. In the gorilla they are always united at their origin, which is from the upper and lateral surfaces of the calcaneus (Pira, No. 1105, No. 47). In No. 47 there was a slight additional origin from the under surface of the cruciate ligament. Four more or less distinct bellies are present, providing tendons for toes I–IV (Bischoff, Deniker, Duvernoy, Hartmann, Hepburn, Owen, Pira, Sommer, No. 1105, No. 47). A tendon for the fifth toe was found in but one out of eight gorillas (Keith, 1899). The tendons for II–IV are prolonged, as in man, as parts of the extensor aponeuroses (Hepburn, Pira, No. 47). That to the hallux inserts on the base of the basal phalanx (Duvernoy, Hepburn, Pira, No. 47). Because of its transverse course toward the great toe, the inner belly becomes nearly a separate muscle.

The origin and insertions of this muscle in man are normally as in gorillas, and there are tendons for toes I–IV. A belly for the little toe may very rarely be present. Le Double cites instances in which only three tendons were present: for toes I–III, or for II–IV, or for I, III and IV, or for I, II and IV. Similarly he states that only two tendons, for I and IV, or for II and IV, may be found, or only one tendon, for III, or for IV. He also found the entire muscle absent in one foot of a cadaver which he dissected; the other foot was normal.

Other Primates show in general a similar origin for the muscle, with slight variations. Kohlbrugge notes that, in apes and monkeys, it may sometimes arise in part from other bones than the calcaneus (cuboid, cuneiforms, *naviculare*, and metatarsals). Similar points of origin may occur in prosimians (Murie and Mivart).

In the chimpanzee there are usually four tendons, for I–IV, as in my specimen. A tendon for the fifth toe may, however, be present. According to Keith (1899), this occurred in four out of eleven animals. Tendons for I–IV were present in my orang. But the fifth toe may occasionally receive a tendon (Kohlbrugge). Similarly, in *Hylobates pileatus* I found tendons for I–IV, which is the rule for gibbons, but Kohlbrugge also found a tendon for V in *Symphalangus syndactylus*.

Old World monkeys have tendons for toes I–IV. This arrangement occurs in *Papio sphinx*, *Lasiopyga* and *Pithecus* (Bischoff, 1870), in *Colobinae* (Kohlbrugge), in *Lasiopyga griseoviridis*, *Cercocebus aethiops* (*fuliginosus*), *Pithecus irus*, *Simia sylvanus* (*Inuus ecaudatus*), and *Papio cynocephalus* (Ribbing), and in *Pygathrix germaini* (Straus).

Similarly, in New World monkeys there are usually tendons for digits I–IV, as in *Pithecia monacha* and *Callithrix penicillata* (Bischoff), in *Brachyteles arachnoides*, *Cebus fatuellus* and *Callithrix jacchus* (Ribbing). But in *Ateles* the hallux may receive no tendon (Kohlbrugge).

The number of toes supplied by the short extensor varies greatly in prosimians. Murie and Mivart note the following arrangements: there are tendons for toes I–IV, as in most other Primates, in *Lemur catta* (right foot), *Galago crassicaudatus*, *G. alleni* and *Nycticebus coucang* (two bellies for toe IV in *Nycticebus*); for II–IV, the hallux receiving no tendon, in *Lemur catta* (left foot), *L. variegatus*, *L. nigrifrons* (left foot) and *Chiromys* (*Daubentonia*) *madagascariensis*; for I, II and III in *Daubentonia* (Owen's specimen); for I, II and V in *Lemur nigrifrons* (right foot); and for I and II in *Galago garnetti* and *Perodicticus*. The origin was partly from the fibula in *Lemur*

fulvus. In the specimens of *Daubentonia madagascariensis* studied by Zuckerkandl and by Oudemans, the hallux received no tendon, but those for toes II–IV were present in both instances. Ribbing found tendons for II and III in *Lemur mongoz*, for II–IV in *Lepidolemur*, and for I–IV in *Tarsius*. Ruge (1878a) found tendons to all five toes in *Loris tardigradus* (*gracilis*). Burmeister, Allen and Woollard found only tendons for I–III in *Tarsius*. In my galago there were tendons to all the toes, but only four muscle-bellies, the outermost belly giving off two tendons for IV and V.

In the highland gorilla (No. 47), there is, as I have already described, a fifth belly of the short extensor. This is very much smaller than any of the others. It arises between the bellies for toes I and II and its fibres are continuous with those of the second dorsal interosseus. Ruge (1878a) has described unions of the short extensor and the dorsal interossei in *Loris tardigradus* and the orang. He also studied (1878c) this union in man, in whom it occurs not too rarely. Such a union he regards as a progressive variation.

The phylogenetic history of the short extensor has been traced throughout mammals by Ruge (1878a). He believes that the entire muscle originally arose from the fibula, as he found it in Monotremes, and that there ensued a gradual migration to the dorsum of the foot, with a complete loss of the original peroneal relations. This migration began on the inner side of the foot, until, as in man, apes, and monkeys, the four inner bellies had attained a purely pedal origin. The occasional occurrence of a short extensor belly for the fifth toe, as he found in *Loris tardigradus*, would indicate a complete migration of all of the elements. The *peroneus digiti V* (which Ruge calls the *extensor brevis digiti V*), present in most mammals, he regards as the outermost tendon of the short extensor, which has retained its original position. It arises from the fibula and sends a slender tendon to toe V. This *peroneus digiti V* is normally absent in man, and in him, as in the anthropoids, according to Ruge, the muscle-belly has fused with that of the *peroneus brevis*.

The researches of Frets (1907, 1908, 1911), and those of Ribbing, have led these workers to disagree with the conclusions of Ruge. Frets believes that the *peroneus digiti V* cannot be regarded as the outlying portion of the *extensores breves*, for it may be present along with a short extensor belly for the fifth toe. He cites such cases in prosimians (1907). Likewise, a *peroneus digiti IV*, arising from the fibula, and going to toe IV, may also occur together with a short extensor belly for that toe. In my galago there was a *peroneus digiti V* and also a short extensor tendon for digit V. The latter did not, however, arise from a separate belly, but was of the nature of an accessory tendon from that which went to toe IV. Ribbing does not believe that the short extensor has wandered from the leg to the dorsum of the foot, but that it has always been a pedal muscle. It is needless to go into the details of his argument here, but I would state that he homologizes the mammalian short extensor with a pedal group of muscles found in other Tetrapods. The *peronei digiti IV* and *V* (which he calls *extensores laterales IV* and *V*) he regards as distinct from the short extensor group.

M. peroneus longus. Very few authors describe the insertion of this muscle in the gorilla. It is on the plantar surface of the base of the first metatarsal alone (Duvernoy, Hepburn), or on the first metatarsal and *cuneiforme I* (Pira), or on the first metatarsal and outer dorsal surface of the cuboid (No. 47). In No. 47 the metatarsal insertion was the primary one. In addition to these attachments, the ten-

don was attached by a tendinous plate in the peroneal sulcus of the cuboid. Chapman, Deniker, Owen and Sommer merely state that in their gorillas the muscle is as in man.

The *peroneus longus* normally inserts in man on the base of the first metatarsal, and also on the first cuneiform. It may sometimes also be inserted on the base of *metatarsale II*, or on *metatarsalia III* and *IV*, or on the tendon of the *tibialis posterior* (Le Double). The same author notes that the attachment may be confined to the hallucal metatarsal alone. Testut states that there may be a supernumerary insertion on *metatarsale V*.

In my chimpanzee the insertion of the muscle was limited to the base of *metatarsale I*. Bischoff (1870) and Hepburn found a similar attachment in their animals. A tendinous sheet may hold down the tendon in the peroneal sulcus (Straus).

I found the *peroneus longus* in the orang inserting on the base of the first metatarsal, but there was an additional insertion to the outer side of the cuboid, and the tendon was attached in the peroneal sulcus by a fibrous sheet. In other orangs the tendon may be limited to the base of the hallucal metatarsal (Bischoff, 1870; Hepburn), but a supernumerary insertion on the tuberosity of the fifth metatarsal is not very rare (Kohlbrugge).

In the gibbons the usual insertion is on *metatarsale I* alone (Bischoff, 1870; Hepburn; Kohlbrugge). But I found an additional small tendon to the base of *metatarsale V* and the cuboid in *Hylobates pileatus*.

The insertion in Old World monkeys may be limited to the base of the first metatarsal, as in *Papio sphinx*, *Lasiopyga* and *Pithecus* (Bischoff, 1870) and in *Colobinae* (Kohlbrugge), or the insertion may be chiefly on *metatarsale I*, with an accessory connection to the base of *metatarsale V*, as in *Lasiopyga griseoviridis*, *Cercocebus aethiops*, *Pithecus irus*, *Simia sylvanus* and *Papio cynocephalus* (Ribbing) and in *Pygathrix germaini* (Straus). In my *P. germaini* the tendon was also bound down in the peroneal sulcus of the cuboid.

In New World monkeys the insertion may be confined to the base of *metatarsale I*, as in *Pithecus monacha* and *Callithrix penicillata* (Bischoff, 1870). Ribbing, on the other hand, found also an attachment to *metatarsale V* in *Brachyteles arachnoides*, *Cebus fatuellus* and *Callithrix jacchus*. This insertion was especially strong in *Callithrix*.

The *peroneus longus* insertion seems always to be confined to the base of the hallucal metatarsal in prosimians. Such an attachment was found in *Lemur catta* (Murie and Mivart), in *Daubentonia madagascariensis*, *Lemur variegatus*, *Galago crassicaudatus* and *Loris tardigradus* (Zuckerkandl), in *Lemur mongoz*, *Lepidolemur* and *Tarsius* (Ribbing), in *Tarsius* (Burmeister), in *Tarsius* (Allen), in *Tarsius* (Woollard), and in *Galago* (Straus).

In man a sesamoid cartilage or bone usually occurs in the tendon of the *peroneus longus*, where it curves around the outer border of the foot, in front of the tuberosity of the cuboid. No such sesamoid was present in my specimens of gorilla (No. 47), chimpanzee, orang, gibbon, and *Galago*, but the tendon was thickened at the point where the bone occurs in man. This thickening was especially marked in the orang and gibbon. In *Pygathrix germaini* I found a well-developed sesamoid bone at the usual position. Kohlbrugge found this sesamoid occurring, apparently constantly, in the *Colobinae* and the gibbons which he studied. It has been found in a chimpanzee by Wilder, by Pagenstecher in the drill, and in *Tarsius* by Woollard. Apparently this sesamoid has a rather haphazard occurrence.

Ruge (1878a) came to the conclusion that the *peroneus longus* primitively inserted on the lateral border of the foot (*metatarsale V*) and that its migration across the sole to the base of the first metatarsal was produced by its coming into closer relation with the plantar ligaments. This theory offers an explanation for the supernumerary insertions sometimes found in Primates, and which occur, among the anthropoids, most frequently in the orang. An attachment to the base of *metatarsale V*, or to the cuboid, as occurs in the *G. beringei*, would be regarded as a very primitive type of variation.

M. peroneus brevis. This muscle always shows, in gorillas, the same insertion as in man, on the base of the fifth metatarsal bone (Deniker, Duvernoy, Pira, Sommer, No. 1105, No. 47). It is to be inferred in the absence of detailed descriptions, that Bischoff, Chapman, Hepburn, Macalister and Owen found a similar attachment. All of these writers mention the muscle either as presenting the usual features, or as being as in man.

The prolongation of the *peroneus brevis* as a slender tendon to the fifth toe may occur in the gorilla and other anthropoids, and also in man. This tendon is in reality the terminal portion of the *peroneus digiti V*, and will be discussed with this muscle.

The variations of the *peroneus brevis* in man are of minor interest. They have been discussed by both Testut and Le Double. In my chimpanzee, orang, gibbon, *Pygathrix* and *Galago*, the muscle inserted on the base of *metatarsale V*. The digital prolongation was present in the first three, the complete *peroneus digiti V* in the last two.

The insertion of the *peroneus brevis* exhibits an astonishingly slight variability in Primates, being almost without exception on the base of the fifth metatarsal. Indeed, this would appear to be always the arrangement in the anthropoids and in both Old and New World monkeys (Beattie, Kohlbrugge, Straus). *Metatarsale V* is also the point of insertion in most prosimians (Murie and Mivart, Milne Edwards and Grandidier, Zuckerkandl, Woollard, Straus). Only Burmeister found a different condition. In his *Tarsius* the tendon was inserted on the cuboid. Woollard, however, found it limited to the base of the fifth metatarsal in the same genus.

M. peroneus digiti V (fig. 27). This muscle, or its vestiges, has been described under various names, some of which follow: *peroneus medius* (Cuvier), *peroneus parvus* (Bischoff), *peroneus accessorius* (Henle), *extensor brevis digiti V* (Ruge), *extensor lateralis digiti V* (Ribbing). It is not known to occur as a distinct muscle in the gorilla. It may exist, however, in a vestigial condition. In such instances the terminal portion of the tendon alone is present, associated with the tendon of the *peroneus brevis*. The latter, just prior to its insertion on the base of *metatarsale V*, gives off a narrow prolongation to the fifth toe. It is unnecessary to discuss the reasons for regarding this accessory tendon of the *peroneus brevis* as the vestige of the *peroneus digiti V*, but they are most logical (see papers by Frets). Such a vestigial *peroneus digiti V* has been found in the gorillas of Deniker (both fetus and juvenile), Macalister and Pira. It also occurred in No. 47, the tendon of the *peroneus tertius* being split to allow its passage. In the left foot of No. 47 Morton found a similar tendon, but here it was as a prolongation of the *peroneus tertius*, and not of the *peroneus brevis*. The tendon to the fifth toe which he describes and figures in his young lowland gorilla, and which also was associated with the *peroneus tertius*, is likewise very possibly a remnant of the *peroneus digiti V*. No traces of a *peroneus*

digiti V were found in the gorillas of Bischoff, Hepburn, Ranke, Rothschuh and Sommer. It also was probably absent in the animals studied by Chapman, Duvernoy, Hartmann and Owen, all of whom neither mention nor figure it, although they all discuss the other peroneal muscles. Unfortunately, I have no note of its occurrence or absence in No. 1105. As to its percentage frequency, it has been found, always in a vestigial form, in 35.7 per cent (5 out of 14) of gorillas.

In man the digital prolongation of the *peroneus brevis* tendon is not infrequently present. Le Double found it in 34 per cent (34 out of 100) of Europeans, Wood (cited by Le Double) in 35.3 per cent (36 out of 102),—a frequency practically equal to that in the gorilla. The complete muscle itself may also rarely occur in man (Le Double). Probably the so-called *peroneus quartus* of Otto, arising from the fibula, but which does not reach the fifth toe, and which may sometimes be found in man, is merely a *peroneus digiti V* in which the muscle-belly and proximal portion of the tendon are well-developed, while the terminal portion has become vestigial or disappeared altogether. This would seem to be the view of Frets (1907, 1911) also. He describes what is apparently a typical *peroneus quartus* occurring in the same body with a digital prolongation of the *peroneus brevis* (1911).

The end portion of the *peroneus digiti V* tendon is present as an extension of the *peroneus brevis* tendon in some chimpanzees, orangs and gibbons. As already stated, I found it occurring in my specimens of these animals. In the orang it failed, however, to reach the fifth digit, the weak tendon thinning out into the fascia over the dorsum of the outermost metatarsal.

The *peroneus digiti V* is not, however, always represented in these animals. For example, it has been found in the chimpanzee by Brühl, Champneys, Fick (in three animals, 1925), Hartmann, Humphry, Macalister, Wilder and myself, but not by Bischoff (1870), Hepburn, Michaelis, Ranke, and Rothschuh; in the orang by Fick (1895), Frets (1907), Hepburn, Langer, Michaelis and myself, but not by Bischoff (1870), Ranke, Rothschuh and Ruge (1878a); and in the gibbon by Chudzinski (cited by Sommer), Kohlbrugge (in *Hylobates agilis* and *H. leuciscus*) and myself, but not by Bischoff (1870), Hepburn, Kohlbrugge (*Symphalangus syndactylus*), Ranke (2 animals) and Rothschuh. In the orangs of Fick, Frets, Michaelis and Langer, and in the *Hylobates leuciscus* of Kohlbrugge, the complete muscle, arising from the fibula, but in various degrees of development, was present. In all the others there occurred only the terminal portion of the tendon, prolonged from that of the *peroneus brevis*, and

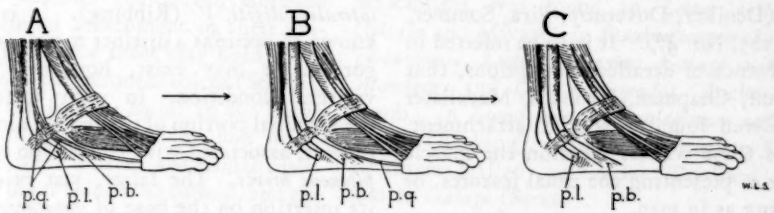


FIG. 27. STAGES IN THE PHYLOGENETIC REDUCTION OF THE PERONEUS DIGITI V MUSCLE IN PRIMATES
A. Complete muscle, arising from fibula. B. Reduction to a prolongation of the peroneus brevis tendon. C. Complete disappearance. *p. q.* = peroneus digiti V; *p. b.* = peroneus brevis; *p. l.* = peroneus longus.

in some instances failing to reach the fifth toe.

In both groups of monkeys and in prosimians a complete *peroneus digiti V* is nearly always present (Beattie; Bischoff, 1870; Burmeister; Frets; Kohlbrugge; Murie and Mivart; Ranke; Ribbing; Woollard; Zuckerkandl; Straus). It may, however, occasionally be absent, as in *Papio cynocephalus* (*Cynocephalus babuin*) (Michaelis), and in *Daubentonia* (*Chiromys*) *madagascariensis* (Owen, cited by Murie and Mivart and by Zuckerkandl). It arises from the fibula in more or less close association with the *peroneus brevis*, and the tendons of the two muscles may be contained in a common sheath, as I found in *Pygathrix germaini*.

Normally its tendon goes to the dorsal aponeurosis of the fifth toe. In Kohlbrugge's *Nasalis larvatus* the insertion was anomalously on the tuberosity of the fifth metatarsal bone. For a most complete account of this muscle in various Primates, the reader is referred to the papers of Frets.

M. peroneus digiti IV. I have found no record of this muscle in anthropoid apes. It occurs rather regularly in prosimians (various authors), and in some monkeys (Frets, Ribbing). In both lower extremities of a human embryo, Ribbing found a well-developed muscle arising on the outer side of the *peroneus brevis*, from the lower portion of the fibula. In the left foot it inserted on the calcaneus; in the right, on *metatarsale V*. Ribbing regards this as homologous with the *peroneus digiti IV* (his *extensor lateralis digiti IV*) of other Primates. It is, more likely, however, nothing more than a *peroneus quartus*, which sometimes occurs in man. This *peroneus quartus*, as previously stated, in all likelihood represents the more proximal portions of the *peroneus digiti V*, and probably has no relation to a true *peroneus digiti IV*.

Nerves. The arrangement and distribution of the nerves in the foot of my highland gorilla (No. 47) is like that of the lowland gorilla (Eisler, 1890; Hepburn; Sommer). In turn, the latter animal agrees with the conditions found in man. The pedal nerves have been but rarely described in the gorilla. The most detailed account is apparently that of Eisler. I have not, however, had access to his article. Those of his findings to which I shall refer have been gleaned from the writings of Kohlbrugge. Hepburn gives a rather full description of the distribution of the nerves in his specimen, while Sommer notes the innervation of the various muscles. The innervation of the *flexor digitorum brevis* is given by Sawalischin for her two gorillas. A passing comment on the plantar nerves is made by Chapman. He merely states that "in a similar manner to that of man, the plantar nerves furnish the nervous supply to the foot of the Gorilla."

The courses of the nerves in Hepburn's animal and in No. 47 agree exactly with the usual arrangement in man. As to the nerve-supply of the individual muscles, in table 4 I have arranged the findings of Eisler, Hepburn and Sommer for comparison with the conditions in No. 47. I have not considered the purely cutaneous branches. It will be noted that the innervation of the muscles varies only in those cases in which variability is encountered in man. Thus, the *lumbricales* show an instability in their nerve-supply. That for toe II is always supplied by the medial plantar nerve, and that for V always by the lateral plantar. The two intermediate *lumbricales* may be innervated by either plantar nerve. The *flexor digitorum brevis* may receive its supply from the medial plantar nerve alone (Hepburn, Sommer, both specimens of Sawalischin, No. 47?), but it may also have a branch from the

lateral pl., as in Eisler's animal. The *flexor digiti V brevis* (and the *opponens digiti V*, when present) and the interosseous muscles of the fourth space are always, as in man, supplied by the lateral plantar nerve, but the fibres to these muscles may be carried by either the superficial or the deep branch of the nerve. The superficial branch of the lateral plantar nerve may contain no motor fibres, as in Eisler's specimen. All of the above-cited variations also occur in man. Eisler found both plantar nerves supplying the *adductor hallucis*. Possibly the fibular head of the *flexor hallucis brevis*, or at least a portion of its anlagen, had fused with the adductor. Hence the double nerve-supply.

Kohlbrugge has summarized and discussed the nerves of the foot in other Primates. These possess the same arrangements as do gorilla and man, and the same variations.

TABLE 4

Innervation of the separate pedal muscles in various specimens of gorillas

	NO. 47	HEPBURN	SOMMER	EISLER
Abd. hall.	Med. pl.	Med. pl.	?	
Abd. dig. V	Lat. pl.	Lat. pl.	Lat. pl.	Lat. pl.
Abd. oss. met. V	Lat. pl. (?)	Lat. pl. (?)	Lat. pl.	
Fl. dig. brev. (superf.)	Med. pl.	Med. pl.	Med. pl.	Med. pl. et lat. pl.
Fl. dig. brev. (deep)	?		Med. pl.	
Lumbrical II	Med. pl.	Med. pl.	?	Med. pl.
Lumbrical III	Med. pl.	Lat. pl. prof.	?	Med. pl.
Lumbrical IV	Med. pl.	Lat. pl. prof.	?	Lat. pl. prof.
Lumbrical V	Lat. pl. superf.	Lat. pl. prof.	?	Lat. pl. prof.
Quad. plant		Lat. pl.		
Fl. hall. br. (*tib.*)	Med. pl.	Med. pl.	Med. pl.	
Fl. hall. br. (*fib.*)	Med. pl.	Med. pl.		
Opponens hall.	Med. pl.	Med. pl.		
Add. hall.	Lat. pl. prof.	Lat. pl. prof.	Lat. pl. prof.	Lat. pl. et med. pl.
Fl. dig. V brev.	Lat. pl. prof.	Lat. pl. superf.	Lat. pl.	Lat. pl. prof.
Opp. dig. V		Lat. pl. superf.	Lat. pl.	
Int. plant	Lat. pl. prof.	Lat. pl. prof. et superf.	?	Lat. pl. prof.
Int. dors.	Lat. pl. prof.	Lat. pl. prof. et superf.	?	Lat. pl. prof
Fl. fibularis	?	Tib.	Tib.	
Fl. tibialis	?	Tib.	Tib.	
Tib. post.	?	Tib.	Tib.	
Exts. hall. et dig. brev.	Per. prof.	Per. prof. (?)	?	
Ext. hall. long.	?	Per. prof. (?)	Per. prof.	
Ext. dig. long.	?	Per. prof. (?)	Per. prof.	
Per. tertius	?		Per. prof.	
Tib. ant.	?	Per. prof. (?)	Per. prof.	
Per. long.	?	?	Per. superf.	
Per. brev.	?	?	Per. superf.	

CONCLUSIONS

The foot musculature of the lone specimen of the highland gorilla, *G. beringei*, falls, in practically all its details, well within the range of variation exhibited by

the known examples of the lowland gorilla, *G. gorilla*. The most striking difference lies in the arrangement of the long flexors, but, as I have pointed out, this should be regarded as a variation of exceedingly primitive pattern. Certainly it can hardly be viewed as a peculiarity of the highland species; at least, not until more highland gorillas have been dissected, and until further lowland gorilla feet are thoroughly studied. Similarly, the accessory attachment of the *peroneus longus* tendon to the outer border of the foot falls in the category of atavistic variations. Possibly the little muscle of the deepest plantar layer, which yokes the second and third toes, and which occurs only in the two *G. beringei*, will eventually be found to be a peculiarity of this species. But in this, as in other points, we cannot be certain until more examples of both species, and particularly of *G. beringei*, have been carefully studied.

If it is finally shown that the foot musculature does differ in the two forms, I think it safe to predict that such a difference will only be an average one. Keith (1899) has shown that this is largely true in respect to the differences in the foot muscles of the gorilla and the chimpanzee. We can therefore hardly expect any striking differences between the two gorilla species.

The foot musculature of the gorilla makes a closer average approach to that of man than does the foot musculature of the chimpanzee. This seems most likely to be a convergence caused by the habits of the gorilla, and is not to be regarded as indicating a closer genetic relationship to man. Whereas the chimpanzee is essentially an arboreal animal, the adult gorilla, probably at least in part because of its huge size, has become almost wholly terrestrial. Such a change in mode of life has led to convergences towards the human form, none of which are more striking than in the foot. But even so the general plan of the gorilla foot is essentially that of an arboreal Primate, and in some respects it is highly specialized in a different direction than that of man. The orang, on the other hand, has become very highly adapted to a purely arboreal life, and in consequence has undergone certain specializations peculiar to itself. Naturally the foot shows changes, not only in the skeleton, but also in the muscles, e.g., the complete elimination of the long hallucal flexor tendon and the development of an *opponens hallucis*. These specializations are almost certainly associated with the reduction of the great toe in the orang. In most characters of the foot the orang is further removed from man than are the chimpanzee and the gorilla, in a few it is closer. On the whole it is highly specialized in its own direction. The gibbon foot is intermediate between the typical Old World monkey foot and those of the great apes. In some characters, as in the flexor muscles, it is more like the monkeys; in others, as in the deep plantar muscles, it is more like the great apes. The general plan of the foot musculature of both Old and New World monkeys is more primitive than that of the anthropoids and man. The typical prosimian foot is in some characters like that of the typical monkey, in others more primitive, and in still others extremely specialized in its own direction. The prosimian foot thus in no sense stands in linear relationship to those of other Primates, but is in general a structure specialized along its own lines.

The reader has probably already noted that in some of the foot muscles there exist, on the whole, but little if any differences among Primates. These muscles are to be regarded as very primitive and conservative in their structure, and hence can yield but little evidence in any study of the evolution of the Primate foot.

Certain groups of muscles, however, show a wide range of variability and differ markedly among the various Primate groups. Such muscles are the long and short flexors of the toes, the deep plantar muscles, and to a less extent the peroneal group. A thorough study of these will reveal the important changes which have taken place in the Primate foot.

In conclusion, I would again state that, in its musculature, as in its skeleton and outer form, the foot of the gorilla more closely approaches that of man than does the foot of any other Primate. But at the present time it is very difficult to decide which of these similarities are indications of close genetic relationship, and which are merely due to convergence produced by interaction of environmental forces and an ancient, basic ground plan.

LIST OF LITERATURE

ADACHI, B. 1910. Beiträge zur Anatomie der Japaner. XII. Die Statistik der Muskelvarietäten. Zschr. f. Morphol. u. Anthropol., XII, 261–312.

ALLEN, H. 1898. Observations on *Tarsius fuscus*. Proc. Acad. Nat. Sci., Philadelphia, 34–55.

BARDEEN, C. R. 1907. Development and variation of the nerves and musculature of the inferior extremity and of the neighboring regions of the trunk in man. Amer. Jour. Anat., VI, 259–390.

BARNARD, W. S. 1875. Observations on the membral musculation of *Simia satyrus* and the comparative myology of man and the apes. Proc. Amer. Assoc. Adv. Sci., 112–144.

BEATTIE, J. 1927. The anatomy of the common marmoset (*Hapale jacchus* Kuhl). Proc. Zool. Soc. London, 593–718.

BISCHOFF, T. L. W. v. 1870. Beiträge zur Anatomie des *Hylobates leuciscus* und zu einer vergleichenden Anatomie der Muskeln der Affen und des Menschen. Abhandl. d. Math.-Phys. Cl. d. königl. Bayerischen Akad. d. Wissensch., X, 3. Abth., 198–297. (*Hylobates leuciscus*, chimpanzee, orang-utan, *Macacus cynomolgus*, *Cynocephalus maimon*, *Cercopithecus sabaeus*, *Pithecia hirsuta*, *Hapale penicillata*.)

———. 1880. Beiträge zur Anatomie des Gorilla. Abhandl. d. Math.-Phys. Cl. d. königl. Bayerischen Akad. d. Wissensch., XIII, 3. Abth., 1–48. (Gorilla).

BRÜHL. 1871. Myologisches über des Chimpanse. Wiener med. Wochenschr., XXI. Jahrg. (Cited by Kohlbrugge.)

BRYCE, T. H. 1923. Myology. Vol. II, part 2, of Quain's *Elements of Anatomy*. 11th. ed., 310 pp. New York and London.

BURMEISTER, H. 1846. Beiträge zur näheren Kenntniss der Gattung *Tarsius*. 140 S. Berlin.

CHAMPNEYS, F. 1872. On the muscles and nerves of a chimpanzee (*Troglodytes Niger*) and a *Cynocephalus Anubis*. Jour. Anat. & Physiol., London, VI, 176–211.

CHAPMAN, H. C. 1897. On the structure of the gorilla. Proc. Acad. Nat. Sci., Philadelphia, 385–394.

COOLIDGE, H. J., JR. 1929. A revision of the genus *Gorilla*. Mem. Museum Compar. Zool., Harvard College, L, no. 4, 293–381.

CUNNINGHAM, D. J. 1882. Report on some points in the anatomy of the thylacine (*Thylacinus cynocephalus*), cuscus (*Phalangista maculata*), and phascogale (*Phascogale calura*), collected during the voyage of H. M. S. Challenger in the years 1873–1876; with an account of the comparative anatomy of the intrinsic muscles and nerves of the mammalian pes. Challenger Reports, V (Zoology), part XVI (1881), 192 pp.

DENIKER, J. 1886. Recherches anatomiques et embryologiques sur les singes anthropoides. Foetus de gorille et de gibbon comparés aux foetus humains et aux anthropoides jeunes et adultes. Thèses présentées à la Faculté des Sciences de Paris, 266 pp. Poitiers. (Published as Suppl. de T. III, Arch. de Zool. Exper. et Gén., 2e. sér., 1885.)

DERSCHEID, J. M. 1927. Notes sur les gorilles des volcans du Kivu. Ann. de la Soc. Roy. Zool. de Belgique, LVIII, 149–159.

DOBSON, G. E. 1883. On the homologies of the long flexor muscles of the feet of Mammalia, with remarks on the value of their leading modifications in classification. Jour. Anat. & Physiol., London, XVII, 142–179.

DUCKWORTH, W. L. H. 1915. Morphology and Anthropology. Vol. I, 2nd. ed., 304 pp. Cambridge.

DUVERNOY, G. L. 1855–56. Des caractères ana-

tomiques des grands singes pseudo-anthropomorphes. Arch. du Mus. d'Hist. Nat., VIII, 1–248.

EISLER, P. 1890. Das Gefäss- und periphere Nervensystem des Gorilla. Halle. (Cited by Kohlbrugge.)

———. 1895a. Die Homologie der Extremitaeten. Abhandl. d. Naturforsch. Gesellsch. zu Halle, XIX, 89–344.

———. 1895b. Die Flexores digitorum. Verhandl. d. Anat. Gesellsch., 9. Versamml., 135–145.

ELLIOT, D. G. 1913. A review of the Primates. 3 vols. Monograph I, Amer. Mus. Nat. Hist., New York.

FICK, R. 1895. Vergleichend anatomische Studien an einem erwachsenen Orang-Utang. Arch. f. Anat. u. Physiol., Anat. Abth., 1–100.

———. 1925. Beobachtungen an den Muskeln einiger Schimpansen. Zschr. f. Anat. u. Entwicklungsgesch., LXXVI, 117–141.

FORSTER, A. 1916. Der M. extensor tarsi (Peronaeus tertius?) bei *Hapale jacchus*. Anat. Anz., XLIX, 257–276.

———. 1922. La tubérosité du scaphoide et le jambier postérieur. Arch. d'Anat., d'Histol. et d'Embryol., I, 1–55.

FRETS, G. P. 1907. Die Varietäten der Musculi peronaei beim Menschen und die Mm. peronaei bei den Säugetieren. I. Petrus Camper, IV, 545–586.

———. 1908. Die Varietäten der Musculi peronaei beim Menschen und die Mm. peronaei bei den Säugetieren. II. Morphol. Jahrb., XXXVIII, 135–193.

———. 1911. Der M. peronaeus digiti V superior beim Menschen. Morphol. Jahrb., XLII, 699–714.

FÜRBRINGER, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. II. Jena.

GLAESMER, E. 1908. Untersuchung über die Flexorengruppe am Unterschenkel und Fuss der Säugetiere. Morphol. Jahrb., XXXVIII, 36–90.

———. 1910. Die Beugemuskeln am Unterschenkel und Fuss bei den Marsupialia, Insectivora, Edentata, Prosimiae und Simiae. Morphol. Jahrb., XLI, 149–336.

HAFFERL, A. 1929. Bau und Funktion des Affenfusses. Ein Beitrag zur Gelenk- und Muskelmechanik. I. Die Anthropoiden. Zschr. f. Anat. u. Entwicklungsgesch., LXXXVIII, 749–783.

HALLISY, J. E. 1930. The muscular variations in the human foot. A quantitative study. General results of the study: I. Muscles of the inner border of the foot and the dorsum of the great toe. Amer. Jour. Anat., XLV, 411–442. (This important publication appeared after the present paper went to press. It therefore receives no mention in the text.)

HARTMANN, R. 1886. Anthropoid Apes. 326 pp. New York. (English translation.)

HECKER, P. 1922. Formation du péronier antérieur chez un chimpanze. Arch. d'Anat., d'Histol. et d'Embryol., I, 147–155.

HEPBURN, D. 1892. The comparative anatomy of the muscles and nerves of the superior and inferior extremities of the anthropoid apes. Jour. Anat. & Physiol., London, XXVI, part I, 149–186, part II, 324–356.

HUBER, E. 1925. Der M. mandibulo-auricularis der Säugetiere, nebst weiteren Beiträgen zur Erforschung der Phylogenese der Gesichtsmuskulatur. Morphol. Jahrb., LV, 1–111. (See S. 86–103 for discussion of Fürbringer's nerve-muscle hypothesis.)

HUMPHRY. 1867. On some points in the anatomy of the chimpanzee. Jour. Anat. & Physiol., London, I, 254–268.

HUXLEY, T. H. 1864. The structure and classification of the Mammalia. Med. Times & Gazette, Vols. I and II for 1864.

KEITH, A. 1894. Notes on a theory to account for the various arrangements of the flexor profundus digitorum in the hand and foot of Primates. Jour. Anat. & Physiol., London, XXVIII, 335–339.

———. 1899. On the chimpanzees and their relationship to the gorilla. Proc. Zool. Soc., London, 296–312.

———. 1923. The adaptational machinery concerned in the evolution of man's body. Nature, CXII, No. 2807, 257–268.

———. 1929. The history of the human foot and its bearing on orthopaedic practice. Jour. Bone & Joint Surg., XI, 10–32.

KOHLBRUGGE, I. H. F. 1897. Muskeln und periphere Nerven der Primaten, mit besonderer Berücksichtigung ihrer Anomalien. Verhandel. d. Koninkl. Akad. van Wetenschappen te Amsterdam (Tweede Sectie), V, No. 6, 1–246.

LANGER. 1879. Die Muskeln der Extremitäten des Orang als Grundlage einer vergl. myol. Untersuchung. Sitzungsber. Kais. Akad. d. Wiss. in Wien, LXXIX–LXXX, 3. Abth. (Cited by Kohlbrugge.)

LEBOUCQ, H. 1895. Les muscles adducteurs du pouce et du gros orteil. Arch. de Biol., XXIII, 41–59.

LECHE, W. 1900. Mammalia. VI, 5. Abth., 1169 S. In Bronn's *Klassen und Ordnungen des Thier-Reichs*. Leipzig.

LE DOUBLE, A.-F. 1897. Traité des variations du système musculaire de l'homme et de leur signification au point de vue de l'anthropologie zoologique. 2 vols. Paris.

LOTH, E. 1908. Die Aponeurosis plantaris in der Primatenreihe. Mit spezieller Berücksichtigung des Menschen. Morphol. Jahrb., XXXVIII, 194–322.

———. 1912. Beiträge zur Anthropologie der Negerweichteile (Muskelsystem). Stud. u. Forsch. zur Menschen- u. Völkerkunde, IX, 254 S. Leipzig.

MACALISTER, A. 1874. The muscular anatomy of the gorilla. Proc. Roy. Irish Acad., I, ser. II, No. 9, 501–506.

MECKEL, J. F. 1821–23. System der vergl. Anatomie. Theil III. Halle. (Cited by Kohlbrugge.)

MICHAELIS, P. 1903. Beiträge zur vergleichenden Myologie des *Cynocephalus babuin*, *Simia satyrus*, *Troglodytes niger*. Arch. f. Anat. u. Physiol., Anat. Abth., 205–256.

MILNE EDWARDS, A., and GRANDIDIER, A. 1876. Histoire physique, naturelle et politique de Madagascar. Vol. VI. Histoire naturelle des Mammifères. Tome I. 396 pp. (Anatomy of Indrisinae.)

MORTON, D. J. 1924. The peroneus tertius muscle in gorillas. Anat. Rec., XXVII, 323–328.

MURIE, J., and MIVART, ST. G. 1872. On the anatomy of the Lemuroidea. Trans. Zool. Soc. London, VII, 1–113.

OCHILTREE, A. B. 1913. Some muscular anomalies in the lower limb. Jour. Anat. & Physiol., London, XLVII, 31–34.

OUDEMANS, J. T. 1889. Beiträge zur Kenntniss d. *Chiromys madagascarensis*. Verhandl. d. königl. Akad. v. Wetenschappen, XXVII. (Cited by Zuckerkandl.)

OWEN, R. 1868. On the anatomy of vertebrates. Vol. III. Mammals. London.

PAGENSTECHER, H. A. 1867. Mensch und Affe. Zool. Garten, VIII. Jahrg., 121–137, 161–172.

PIRA, A. 1914. Beiträge zur Anatomie des Gorilla. I. Das Extremitätenmuskelsystem. Muskeln der hinteren Extremität. Morphol. Jahrb., XLVIII, 167–238.

PRIMROSE, A. 1900. The anatomy of the orang outang. Univ. Toronto Stud., Anat. Stud., No. 1, 94 pp.

RANKE, K. 1897. Muskel- und Nervenvariationen der dorsale Elemente des Plexus ischiadicus der Primaten. Arch. f. Anthropol., XXIV, 117–144.

RIBBING, L. 1909. Die Unterschenkel- und Fussmuskulatur der Tetrapoden und ihr Verhalten zu der entsprechenden Arm- und Handmuskulatur. Lunds Univ. Årsskrift, N. F., Afd. 2, V, Nr. 5, 158 S.

——— and HERMANSSON. 1912. Kleinere Muskelstudien. Die distale Extremitätenmuskulatur eines Schimpansen. Lunds Universitets Årsskrift, N. F., Afd. 2, VIII, Nr. 3, 10 S.

ROSENFELD, M. C. 1898. Zur vergleichenden Anatomie des Musculus tibialis posticus. Anat. Hefte, 1. Abth., XI, 359–390.

ROTHSCHUH, E. 1888. Ueber die Fussmuskeln der Primaten und des Menschen. Diss., München. (Cited by Sommer.)

RUGE, G. 1878a. Untersuchung über die Extensorengruppe am Unterschenkel und Fusse der Säugethiere. Morphol. Jahrb., IV, 592–643.

———. 1878b. Zur vergleichenden Anatomie der tiefen Muskeln in der Fusssohle. Morphol. Jahrb., IV, 644–659.

———. 1878c. Entwicklungsvorgänge an der Muskulatur des menschlichen Fusses. Morphol. Jahrb., IV, Suppl., 117–152.

SAWALISCHIN, M. 1911. Der Musculus flexor communis brevis digitorum pedis in der Primatenreihe mit spezieller Berücksichtigung der menschlichen Varietäten. Morphol. Jahrb., XLII, 557–663.

SCHULTZ, A. H. 1927. Studies on the growth of Gorilla and other higher Primates with special reference to a fetus of Gorilla, preserved in the Carnegie Museum. Mem. Carnegie Mus., XI, No. 1, 1–87.

SCHULZE, F. E. 1867. Myologische Untersuchungen. I. Die Sehnenverbindung in der Planta des Menschen und die Säugethiere. Zschr. f. Wissensch. Zool., XVII, 1–22.

SCHWALBE, G., and PFITZNER, W. 1894. Varietäten-Statistik und Anthropologie. III. Morphol. Arb., III, 459–490.

SIRENA, S. 1876. Ricerche della miologia del *Mycetes fuscus*. Giorn. di Sc. nat. ed econom., VII, 1–84. (Cited by Sommer.)

SOMMER, A. 1906. Das Muskelsystem des Gorilla. Habilitationsschrift, Med. Fak. Würzburg, 128 S. Jena. (Also published under same title in Jen. Zschr. f. Naturwissensch., XLII, 181–308, 1907.)

SONNTAG, C. F. 1924. The Morphology and Evolution of the Apes and Man. 364 pp. London.

STRAUS, W. L., JR. 1926. The nature and inheritance

of webbed toes in man. Jour. Morphol. & Physiol., XLI, 427–439.

STRAUS, W. L., JR. 1929a. The interosseous muscles of the foot among Primates. Anat. Rec., XLII, 63. (Preliminary report.)

———. 1929b. The foot musculature of an adult female highland gorilla (*Gorilla beringei*). Anat. Rec., XLII, 64. (Preliminary report.)

SYMINGTON, J. 1890. Observations on the myology of the gorilla and chimpanzee. Rep. Brit. Assoc. Adv. Sci., 1889, 629–630.

TESTUT, L. 1884. Les anomalies musculaires chez l'homme expliquées par l'anatomie comparée. Leur importance en anthropologie. 844 pp. Paris.

TURNER, W. 1867. On variability in human structure, with illustrations, from the flexor muscles of the fingers and toes. Trans. Roy. Soc. Edinburgh, XXIV, 175–189.

WEIDENREICH, F. 1922. Der Menschenfuss. Zschr. f. Morphol. u. Anthropol., XXII, 51–282.

WILDER, B. G. 1862. Contributions to the comparative myology of the chimpanzee. Boston Jour. Nat. Hist., 353–384.

WILLAN, R. 1912. The action of the extensor, lumbrical, and interosseous muscles in the hand and foot. Anat. Anz., XLII, 145–153.

WOOLLARD, H. H. 1925. The anatomy of *Tarsius spectrum*. Proc. Zool. Soc. London, 1071–1184.

ZUCKERKANDL, E. 1898. Zur Anatomie von *Chiromys madagascarensis*. Denkschr. d. Kais. Akad. d. Wissensch. Wien, Math.-Naturw. Cl., LXVIII, 89–200.

THE HYDROGEN-ACTIVATING ENZYMES OF THE CELLS

By T. THUNBERG

Lund, Sweden

1. HEINRICH WIELAND'S NEW CONCEPTION OF CERTAIN OXIDATION PROCESSES

HEINRICH WIELAND, of Munich, the celebrated chemist who in 1928 was awarded the Nobel prize, must be considered as the discoverer of the enzyme group called the dehydrases or dehydrogenases, characterised by their power to activate the hydrogen of certain organic substances so that it will be able to cause reactions, not occurring in the absence of these enzymes.

Of the two terms dehydrases and dehydrogenases, I prefer the latter, for which I myself am responsible. It seems to me that when translated into various languages this term will give rise to fewer mistakes or misunderstandings than any other. The designation "dehydrases" has the advantage of being shorter, it is true, but it may in certain languages easily be taken to mean an enzyme which deprives the substance, not of hydrogen, but of water. This misunderstanding of this scientific term would be natural also on account of the fact that in technical language a substance deprived of water is said to be dehydrated.

The name "redoxases" has also been suggested for these enzymes, by von Euler, Jr. The name is short and is based on the fact that oxidations and reductions are bound up with each other. Any oxidation of one substance implies reduction of something else. To take the simplest instance, when oxygen and hydrogen unite we may speak of the oxidation of the hydrogen to form water, or of the reduction of the oxygen, also to form water. Every oxidase is certainly a reductase and it is quite legitimate to express this fact by means of such a name as redoxase. But in objection to this designation "redoxases" for the group of enzymes which I prefer to call "dehydrogenases," it may be pointed out that the name "redoxases" seems to suggest a wider group of enzymes than intended. It would apply to the enzymes transporting oxygen just as well as to those transporting hydrogen. That is to say, the designation is too wide for the group it is meant to refer to.

Still another name has been proposed, the name "hydrogeno-transportases." I am responsible for this name also. It was suggested for and seems to me to fit particularly those processes which are reversible and characterized by a mutual interchange of hydrogen between two substances and which processes occur under the influence of these enzymes.

In 1912 and 1913 Wieland published a new conception of the mechanism of the oxidation of certain inorganic and organic dysoxidisable substances at low temperatures and without help of such very active agents as strong acids or alkalis. According to his theory the oxidation is due to the activation of the hydrogen of the substances, not as was thought before to an activation of oxygen.

The oxidation theory of Wieland was at first developed in the field of pure chemistry. The simplest example of an oxidation in which we seem to have to assume the activation of hydrogen to be the main factor is the reaction:

$$\text{hydrogen} + \text{oxygen} = \text{water}$$

Pure hydrogen and oxygen do not react with each other with a measurable velocity at lower temperatures. But in the presence of spongy platinum or palladium they do.

$$H_2 + O_2 + (Pt) \rightarrow H_2O_2$$

Then the hydrogen peroxide is split up into water and oxygen, this process being also catalyzed by the platinum:

$$2H_2O_2 + (Pt) \rightarrow O_2 + 2H_2O$$

Earlier, it was believed that this reaction was due to an activation of oxygen with formation of a peroxide of the metal as an intermediary stage. Since, however, hydrogen peroxide has been shown to be the intermediate oxidation product it seems more probable that the hydrogen has been activated, and that the oxygen molecule plays the part of an "acceptor" for the hydrogen activated.

That the hydrogen is activated is demonstrated by the fact that oxygen as hydrogen acceptor can be replaced by other substances, e.g. methylene blue. Methylene blue, (=Mb.) a quinoid dye stuff with no oxygen in the molecule, is reduced by activated hydrogen to colorless leucomethylene blue.

When one bubbles hydrogen through a solution of Mb. no reduction to leuco-Mb. will take place, but if one also adds some spongy platinum the blue color will soon disappear. The hydrogen has been activated and reacts with the dye stuff to form leuco-Mb.

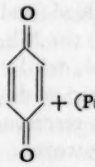
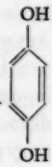
In this case we had to do with an activation of free hydrogen. But bound hydrogen can also be activated in the same way. Let us take the following example: For a long time it has been known that primary alcohols will be oxidized to aldehydes by oxygen in the presence of spongy platinum

$$2CH_3CH_2OH + O_2 + (Pt) \rightarrow 2CH_3CHO + 2H_2O$$

(In the same way as in the last example H_2O_2 is an intermediary oxidation product.)

In this case also there is an activation of hydrogen. The oxygen has the function of a hydrogen acceptor, which can be replaced, for example, by Mb. or quinone.

$$CH_3CH_2OH + Mb + (Pt) \rightarrow CH_3CHO + MbH_2$$

or CH_3CH_2OH +  + $(Pt) \rightarrow CH_3CHO$ + 

As early as 1913 Wieland extended his theory to embrace also certain biological oxidation processes. In that year he was able to show that the acetic acid bacteria are able to oxidise alcohol to acetic acid even in the absence of oxygen, if only a suitable hydrogen acceptor, e.g. Mb. is present. The alcohol is changed into acetic acid and the Mb. is transformed into its leuco-form, which shows that what is called oxidation of the alcohol is in reality a dehydrogenation.

Wieland did not succeed in extracting in soluble form the enzymes, which may be supposed to cause the action of the bacteria on the alcohol.

If we keep up the distinction between, on one hand, pure enzymatic effects and, on the other, protoplasmatic effects depending on the protoplasm structure, Wieland must

be said to have shown that the acetic acid fermentation must be regarded as a dehydrogenation; but at the same time we lack full evidence that this dehydrogenation is effected by enzymes. It might possibly be due to other resources of the protoplasm.

For my own part I may say, that I don't believe much in such a distinction. It is at any rate certain, that this objection does not apply to the mechanism of another biological process, which Wieland investigated in connection with the one mentioned above: viz. the so-called Schardinger reaction.

Fresh milk will not reduce Mb. and if formaldehyde (or some other aldehyde) is added to milk, it remains for long without change. But when both formaldehyde and Mb. are added (and especially, if oxygen is excluded) the Mb. is reduced to the leuco-compound, while the aldehyde is oxidised to formic acid. Boiled milk does not show the reaction, because the enzyme has been destroyed.

Now Wieland was able to show, that in the case of this reaction the aldehyde functions as a "hydrogen donator," if we use the term I later introduced. The hydrogen of the aldehyde or to be more precise, the hydrogen of the hydrate form of the aldehyde, not of the aldehyde itself, is activated by the Schardinger enzyme and this activated hydrogen reacts with the Mb. which is transformed to leuco-Mb. By giving off this hydrogen the aldehyde hydrate is simultaneously transformed to the corresponding acid.

It ought to be mentioned, that a few years earlier Bredig had already interpreted the Schardinger reaction in a similar way. In a paper "Die Schardingersche Reaction und ähnliche enzymartige Katalysen" Bredig and his collaborator Sommer wrote as follows:

> Thus we have found that the inorganic catalysts as well as the milk enzyme very easily transport the oxygen of the methylene blue to oxidisable substances as e.g. formaldehyde. Or, to be more exact, they transport the hydrogen of the formaldehyde to reducible substances such as the dye mentioned above. In reality it is surprising to find there exists a high degree of resemblance between the inorganic catalyst and the milk enzyme in this Schardinger reaction.

At the same time it must be pointed out, in fairness to Wieland, that Bredig never experimented on the real biological enzyme; he pointed out an interesting analogy based on the result of inorganic model experiments and gave a successful interpretation of it. Wieland, on the other hand, worked on the biological enzyme and showed how it was possible for the aldehyde while it functioned in its hydrate form to serve as a source of hydrogen by the decolorisation of Mb.

2. THE APPLICATION OF THE IDEAS OF WIELAND TO THE PROBLEM OF THE OXIDATION OF "METABOLITES" OF HIGHER ORGANISMS. THE "SUCCINO-DEHYDROGENASE"

The examples of biological dehydrogenation brought forth by Wieland concerned bacteria and an extra-cellular enzyme which at that time seemed to be of no great account in the metabolism. The importance of Wieland's ideas for the understanding of the intracellular oxidation processes of higher organisms was first shown by the discovery of other dehydrogenases, able to activate substances, which undoubtedly had a place in the metabolism of the higher organisms e.g. succinic acid, malic acid, citric acid, lactic acid, and glutamic acid.

Of these enzymes it is primarily that acting on succinic acid, i.e., the "succino-dehydrogenase," which has served to bring out characteristics of the group. Some words may be said about its detection.

A quarter of a century ago I began a

series of investigations concerning the respiration of the isolated muscle in its dependence on various factors. Using an apparatus which I had constructed for this purpose, the micro-respirometer, I studied the respiration not only of the intact muscle but also of minced muscle substance. I investigated how the respiration of such muscle substance was influenced by various substances, e.g. the fatty acids and their derivatives.

During the course of these studies I found in 1909 that the oxygen consumption of the muscle substance was increased by the neutral alkali salts of succinic acid.

On the basis of this observation of mine Battelli and Stern, of Geneva, showed that the increase of oxygen consumption, which is caused by succinic acid, corresponds to one atom oxygen per molecule succinic acid. The next step was the discovery by Einbeck that the succinic acid is oxidised by the muscle substance to fumaric acid. The reaction mixture shows also a content of malic acid, which seems to have been formed from the fumaric acid under the influence of a hydrolytic enzyme, discovered by Battelli and Stern and called by them "fumarase". The investigations of Dakin have thrown further light on the nature of this reaction and shown that the malic acid, which is formed from the fumaric acid, is the laevo-form. We have also to thank Dakin for our knowledge of the quantitative conditions in the equilibrium between fumaric acid and malic acid.

However, before the processes in question had been investigated up to this point, the continuation of my own experiments had led to some new results.

The observation that succinic acid is very easily changed into fumaric acid under the influence of animal tissues, was bound to cause surprise. The succinic acid represents the final stage of the oxidation of fatty acids with such an agent as e.g. nitric acid, which means that the succinic acid itself is resistant against these strong oxidation agents. During my attempts to find the explanation why in spite of this fact succinic acid is so easily oxidised in the organism, I came across Wieland's accounts of his investigations referred to above. They seemed to me to furnish a possibility for the explanation I wanted, and as a working hypothesis I postulated that the oxidation of succinic acid in the tissues is made possible by the activation of its hydrogen.

In order to verify this I made the following experiment. In each of two tubes, which could be evacuated, I placed equal quantities of muscle substance and of Mb. In one of the tubes I further placed some succinic acid in the form of its neutral potassium salt. The tubes were then evacuated and placed in a thermostat at 35°C.

The two tubes behaved quite differently. The tube which did not contain succinic acid showed no change in its color, while the mixture in the other tube soon had been wholly decolorised.

Since the Mb.-decoloration requires the presence of activated hydrogen this result fully proved that succinic acid under the influence of the enzymes of the muscle tissues is activated in regard to its hydrogen. The only reaction product which can very well be imagined to occur under these circumstances is fumaric acid.

Afterwards several investigators have proved by direct analysis that fumaric acid is formed from succinic acid by the influence of the dehydrogenases in spite of the absence of oxygen if only a suitable other hydrogen acceptor is present (Quastel & Wetham, using bacteria, 1924; Gottwalt Fischer, using muscle substance, 1927; and Hahn & Haarmann, also using muscle substance, 1927).

Having found that the oxidation of such a substance as succinic acid by animal tis-

sues is begun by an activation of its hydrogen, I went on to investigate if, or to what extent, a similar mechanism played a part in the oxidation of a certain number of other substances, and how the hydrogen-activating power of the cells and their enzymes was influenced by various factors.

The field of the investigations planned was wide and in order to make it possible to cover it in available time I first elaborated a convenient and handy method. The method is now used in many other laboratories than my own. I think it was the Cambridge school, which gave it the name "The Thunberg technique."

3. THE "THUNBERG TECHNIQUE"

The most important constituents of the Thunberg technique are the vacuum test tubes. "Thunberg-tubes" serve while keeping out oxygen to contain the reaction mixture, in which the hydrogen activation is going on, and in which also an indicator for activated hydrogen is present. Keeping out the oxygen is necessary for two reasons. If oxygen is present it may work as a hydrogen acceptor. The active hydrogen divides then between the oxygen and the indicator according to unknown laws, the reaction velocities and the affinities being the deciding factors. Other factors are the concentrations of the two acceptors, which concentrations vary during the course of the experiment. By keeping the oxygen absent the undesirable accessory reaction with this substance is eliminated. The total quantity of hydrogen formed during the reaction in that way is taken over by the indicator and kept by it.

Only when the experiment is carried out in the absence of oxygen is it practicable to use as indicators substances, e.g. methylene blue, the reduction forms of which are oxidised by oxygen.

A Thunberg tube is a glass tube usually holding about 10 cubic centimeters, one end of which is closed, while the other is open. The open end can be closed by means of a stopper of conical form and fitting very closely. A hole in the stopper can be made to communicate with a side-tube closed by turning the stopper. This side-tube can by a rubber-tube be put into communication with a vacuum pump.

In order to prevent air or water from penetrating into the vacuum tube after its evacuation it is necessary to treat the stopper with a good vacuum grease. [3 parts Adeps lanae (= dehydrated lanolin), 2 parts Vaselinum and 3 parts Bees wax are melted together and stirred during the cooling, so that a homogeneous grease is obtained.]

After the evacuation the vacuum tube is placed under water in a thermostat. One side of this thermostat is made of glass so that it is possible to observe the vacuum tubes. The other parts of the inside of the thermostat are painted white in order to facilitate the observation of the color changes of the vacuum tubes.

The temperature of the thermostat is kept constant within a range of 0.1°C. by a good thermo-regulator (e.g. an Ostwald toluol regulator).

The vacuum tubes must be protected against too strong light since otherwise the decoloration would be accelerated. Precautions must be taken so that some tubes are not subjected to stronger light than others. The thermostat is best placed in a fairly dark corner of the room, a special lamp being lighted for the moment of observation.

As indicator on the activated hydrogen different substances can be used. Methylene blue has been used more extensively than any other. A few words about this substance may therefore be said.

This valuable dye was discovered by Caro in 1876 and has since then been widely

used in the dye industry. As early as 1885 Dreser introduced it in the biological technique for certain biological reaction processes. Wieland utilized it in his first experiments in 1913 with the dehydrogenases and since then it has been constantly used for these studies.

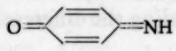
Mb. is a compound free from oxygen and formed by two six-membered rings of carbon atoms bound together by a six-membered ring containing one nitrogen atom and one sulphur atom. It belongs to the group of the thiazin substances and may be regarded as a derivative from another well-known dye, Lauth's violet, or thionin. Mb. is tetra methyl thionin.

Mb. belongs to the very wide group of dyes, which all may be characterized as quinonimid dyes. Certain of these have their imid group acyclically bound, e.g. the indophenols and indamins. To the compounds with a cyclically bound imid-group belong e.g. the thiazins. The quinone-imid part of the molecule is of greatest account for the dye character of these substances. That their tendency to act as dyes is actualized is due to the entrance in the molecule of what is called auxochromatic groups. The NH_2 group functions as such in the thionin and its derivatives, e.g. Mb.

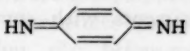
A point of interest is the question of what changes take place in the Mb. molecule when, under the influence of a reducing agent, it is changed to its leuco-form. Generally this reaction is expressed in the following simple way:

$$Mb + H_2 = MbH_2$$

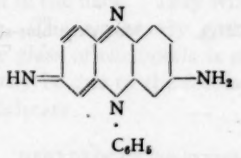
This equation is permissible for some practical purposes but is open to the objection that it will easily cause misunderstandings. It must not be taken to mean that the ring structure remains unchanged



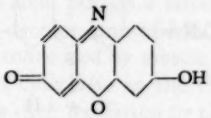
Chinon-monimid



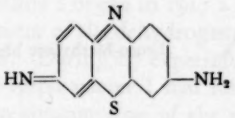
Chinon-diimid



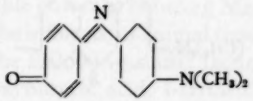
Phenosafranin



Resorufin



Thionin



Phenolblau

Dimethyl-phenylengrün

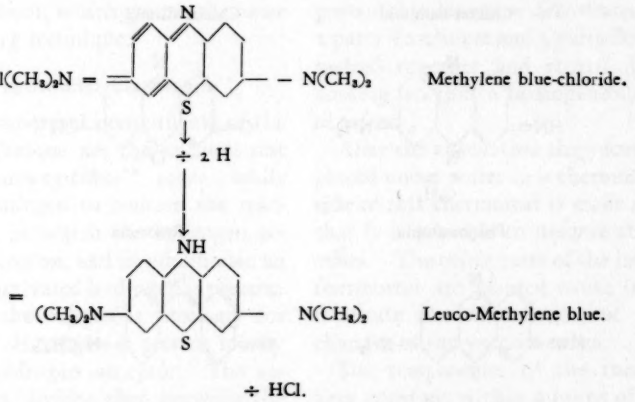
when Mb. is reduced. As a matter of fact the quinoid binding with its two double bonds is changed to a benzoid binding. Since the dye character depended on the quinoid binding it is obvious that in this way the substance must be decolorized.

The equation given above seems to express the introduction of two hydrogen atoms in the Mb. molecule. This needs to be explained.

When speaking of Mb. experiments we mean in reality experiments with some Mb. salt usually the Mb. chloride. There is no need to discuss here how the Mb. chloride is transformed in the phosphate solution used for dehydrogenase experiments. It seems likely that Mb. appears as an ion both in the pure water solution of its chloride and in the phosphate solution. In any case the chemical equation expressing the transformation of Mb. under the influence of reducing agents can be based on the salt formula. The more simple formula given above will then appear in the following form:

$$MbCl + H_2 = MbH_2Cl$$

It may be objected that although the constitution of the Mb. molecule allows the formation of a chloride, this is not the case with the leuco-Mb. molecule. But it may on the other hand possibly give rise to a hydrochloride. This hydrochloride of leuco-Mb. will however rapidly and to a great extent dissociate giving off hydrochloric acid with change of the 5-valent nitrogen to 3-valent. Thus, if Mb. is reduced—for which reduction two atoms of hydrogen are necessary—we obtain one molecule Mb.H and in addition one molecule free hydrochloric acid. Notwithstanding the different final fates of the two H-atoms in question, we may very well use the short formula given above, since we are entitled to assume that the leuco-Mb.-HCl appears at least as a transitory product.



Mb. is available either as a chloride or as a zinc double chloride. Only the chloride is to be used as indicator. Not a few mistakes are probably to be put down to the unintentional use of the zinc double-chloride.

Mb. is easily dissolved in cold water. Even in the case of dilute solutions, as 1:5000 or 1:1000, Mb. dissolves only slowly, and on account of this the solution ought to stand at least one day before being used.

The leuco-Mb. (= LMb.) is not so soluble as Mb. In acids LMb. is soluble to about 0.5 millimolar (= 1:5000), and in alkaline solutions to about 0.02 millimolar (= 1:125000). By reduction of a concentrated solution of Mb. the resulting LMb. gives a precipitate. If this fact is unknown to the experimenter he very easily puts a false interpretation on the precipitate formed in the reaction mixture during an experiment.

Before starting a series of experiments it is a good plan to make ready 100 cc. of the various concentrations 1:500, 1:1000, 1:1500, 1:5000, and 1:10000. The solutions must be kept in the dark. They will keep for months. The apparently great adsorption on the glass of the bottle is of no account. It may be due to the formation of some Mb-Silicate.

4. THE GENERAL DEHYDROGENASE-SYSTEM OF THE ANIMAL TISSUES

With this method I began in 1917 a series of investigations of the dehydrogenases of animal tissues. During my experiments with my micro-respirometer I had found that the oxygen consumption of the surviving, perfectly fresh frog muscle substance was strongly increased under the influence of malic acid, fumaric acid, and citric acid. I now began to investigate whether the hydrogen of these substances is activated, when they are added to muscle substance in vacuo.

Such fresh muscle substance already possesses a strong decolorisation power independent of every extra addition of donator substance, which decoloration obviously must be due to donator substances already present in the system. This spontaneous decoloration makes it often difficult to observe a possible decoloration-effect caused by the addition of other donator substances.

In order to avoid this difficulty I extracted the fresh muscle substance with water, or some suitable salt solution, and thus, by depriving it of at least the greatest part of its preexisting donators which is possible without extracting the enzymes at least to the same degree, brought the spontaneous decoloration down to a minimum of no importance. I then used this extracted muscle substance for the investigation of the substances mentioned above and of a great number of other substances.

The results of these experiments showed that the before-mentioned three substances: malic acid, fumaric acid, and citric acid, possess a strong power to cause the decoloration of Mb. in vacuo, if they are influenced by muscle substance. Thus it is clear also in the case of these acids that their oxidation by the tissues is begun by the activation of their hydrogen.

Among the considerable number of other substances investigated I found a considerable power of reducing Mb. in vacuo under the influence of animal tissues in the case of the following acids: lactic acid, α- and β-oxybutyric acid, l-tartaric acid, mesotartaric acid, α-oxyglutaric acid, and glutamic acid.

In my analysis of these facts and especially of the catalytic factors in question I wrote as follows (For reasons given below I will give here a word for word translation of this part of my paper.):

> The reduction processes which have thus been discovered are in all probability of enzymatic nature.
>
> It is obvious, to begin with, that for these processes some compounds of the cell are necessary. If the salts of the above-mentioned organic acids are mixed only with Mb., no decoloration process takes place. This only happens when tissue substance is added to the mixture. In order for such decoloration to take place the tissue substance washed in the way previously described is insufficient.
>
> The necessary factors are: 1. the presence of one factor in the cell substance, 2. the donator substance,

3. Mb. or some other acceptor susceptible to hydrogen. Thus the reaction is obviously bound to what may be termed a chemical three-compound system, or, to be precise, a catalytic three-compound system.

Somebody might ask whether the supposition of such a three-compound system does not mean a simplification of the actual conditions. More components than suggested by this name might be necessary for the reaction. Further, is not the necessary cellular factor of so complicated a nature that it cannot be called an enzyme but must be looked upon as belonging to the normal cell-structure.

However, what the cell structure seems to be able to effect in preference to a simple physical-chemical system, is a harmonic course of the continuous links of a long reaction chain, and, further, the transformation of chemical energy into other forms of energy, e.g. mechanical energy (*via* surface tension changes or imbibation changes), electrical energy, osmotic energy, etc. But there is no reason to suppose that in order to take place a simple chemical process would require the presence of a cellular structure. The deletary conditions to which muscle mass has been subjected speak against the supposed importance of the cell structure to the reactions in question. The mincing of the muscle cells and the treatment with distilled water are factors which must derange the polyphasic system of the muscle cells, i.e. their structure.

Thus there is every reason to suppose that these decoloration phenomena are vital not in the sense that they demand the preservation of the cell structure but only in that they require the presence of the enzymes active in the cells. Conceded that these processes are of enzymatic nature, the question will be: have we here a single enzyme with general effect or are there many enzymes, each with its specific effect?

In one respect there is no doubt about the answer. The succino-dehydrogenase must be a specific enzyme. On account of its great resistance it can easily be obtained free from other dehydrogenases.

Obviously only experimental investigations can solve the question whether one or several enzymes are responsible for the other dehydrogenations which have been observed besides that of the succinic acid. One reason in favor of several enzymes is the decided specificity typical of the succino-dehydrogenase. The conclusions which might possibly be drawn from this fact, point to other enzymes in the enzyme mass being of a fairly well-pronounced specificity.

But this must not be regarded as indicating absolute specificity. Already in the case of succino-dehydrogenase I have found that not only the succinic acid can be activated. Under the influence of the succino-dehydrogenase even methylsuccinic acid will show some power of decolorizing methylene blue.

Consequently it is not impossible that the dehydrogenases form a group of enzymes of which each individual influences its own metabolite, or perhaps a small group of such substances, or possibly, of other related substances.

With help of the Mb.-technique described above other tissues than muscle were also investigated in my laboratory. The result was that all tissues contain dehydrogenases. Here only the results in some special cases may be mentioned.

5. THE DEHYDROGENASES OF THE WHITE NERVE SUBSTANCE

It is a well-known fact that science has long hesitated to ascribe to the white nerve-substance an oxygen consumption. But in 1903 certain German investigators: Garten, v. Baeyer and Fröhlich, gave indirect proofs that such consumption must be assumed. In 1904 I was able to give direct proofs with the help of my microrespirometer that such consumption of oxygen is going on and even to ascertain, at least approximately, the quantity consumed. Some years later, in 1923, I tried to find out whether the mechanism of this oxygen consumption is the same as in the case of other tissues. Using my Mb. method I showed that the usual dehydrogenases are present in the white nerve-substance also. The dehydrogenases of the nerve are thus able to activate succinic acid, glycerinphosphoric acid, lactic acid, citric acid, glutamic acid, and α- ketoglutaric acid. Contrary to what happens in the case of muscle substance, glycerinphosphoric acid is more strongly activated by the white nerve-substance than succinic acid is.

The fact that citric acid is activated by the white nerve-substance is doubly interesting considering that citric acid is

present in the cerebrospinal fluid, as will be shown below.

6. THE LENS SYSTEM

Dehydrogenases are also to be found in the lens, an organ, which as we now know, shows a small but certain oxidative metabolism.

Dehydrogenases effecting the oxidation of fumaric, malic, glycero-phosphoric, lactic, citric and acetic acids and the amino-acids alanine and valine have been found by Ahlgren to exist in the lens.

The lens was, however, lacking in succino-dehydrogenase, which enzyme has been observed in all other tissues tested. This would seem to indicate that the metabolism in the lens to a certain extent follows a different path from that of muscles and other tissues. The lens-cortex showed a greater oxidation intensity than the lens-nucleus.

From my investigation of the dehydrogenases I concluded that *these enzymes are chemical tools of universal importance in the life of every cell.* This leads to the question to what extent this discovery must change our conception of the metabolic processes in the cells and, more particularly, of the oxidative destruction of the food stuffs. When trying to find the answer to this question I was driven to contradict the current views of the genetic relation between the free oxygen from the atmosphere and that bound in the carbon oxide formed by the living cells.

7. GENERAL VIEW OF THE FINAL FATE OF THE CONSUMED OXYGEN AND OF THE ORIGIN OF THE OXYGEN IN THE EXPIRED CARBON DIOXIDE

Two questions of interest here are: *1.* What is the ultimate fate of the *free* oxygen which we breathe, i.e. which are its final products? and *2.* What is the origin of the oxygen forming part of the carbon dioxide which we give off? According to current physiological views the answers to these queries are as follows. The most important final product of the consumed free oxygen is the carbon dioxide. Only a small part of the oxygen takes the form of water. The proportion between the part of the consumed oxygen found in the expired carbon dioxide and the part which has formed water is reflected in the respiratory quotient.

The term "respiratory quotient" was coined by Pflüger in 1877 and defined by him as the relation between the oxygen in the carbon dioxide and the oxygen consumed at the same time. Soon afterwards Zuntz in his standard work on the respiratory metabolism in Hermann's Handbook wrote as follows. "When by the oxidation of carbon one volume oxygen gives one volume carbonic acid the respiratory quotient shows clearly how much of the oxygen consumed is used in the oxidation of carbon and how much goes to that of other substances, especially hydrogen."

According to my opinion we have to change fundamentally our views on these things. I consider that nothing of the oxygen consumed in the general metabolism is found in the expired carbon dioxide. I consider the catabolism of the food stuffs to take place in a series of continuous dehydrogenations, carried out by a series of dehydrogenases. This procedure, to which the complicated food-stuff molecules are thus subjected, might be compared to what happens in modern factories where a piece of metal glides along on rails from workman to workman each of whom has his special task to carry out in the course of the work until the metal piece leaves their hands as a finished product.

When oxygen is present the hydrogen split off by the dehydrogenases is transported to this oxygen with formation of water.

This oxidative catabolism of the food stuffs is characterised not only by this series of dehydrogenations but also by two other processes, viz. addition of water and the splitting off of carbon dioxide. Through the addition of water the intermediate product of the catabolism receives two atoms hydrogen and one atom oxygen. When the water has been added a new dehydrogenation process takes place and two atoms hydrogen are split off once more. Thus the result is a product which in comparison with the original substance is richer in carbon and poorer in hydrogen and which also shows a change in the proportions between carbon and oxygen in favor of the latter element. Through the splitting off of the carbon dioxide the chain of carbon atoms is shortened step by step.

According to this view of the intermediate metabolism, the food stuffs take part in it on account of their actual or potential content of hydrogen. The carbon of this carbon chain has the same function with regard to the hydrogen as the string for the pearls on it. Although the carbon is never directly oxidised in the metabolism its caloric content and its energy is made available through water addition and the splitting off of hydrogen and its oxidation. For the total fund of energy it is of no importance in what way the oxidation is carried out.

I shall now return to the question referred to above concerning the final products of the oxygen and the origin of the oxygen found in the expired carbonic acid.

With regard to the fate of the oxygen the answer to this question is that the oxygen is used for the oxidation of the hydrogen which is activated by the dehydrogenases and given over to the oxygen in activated form. *The oxygen consumed during the respiration is transformed to water.*

Hydroperoxide must be the first, or at least the most important product of this reaction between hydrogen and oxygen. It is the most natural combination product of hydrogen and oxygen in the form available here. However, the formation of hydroperoxide means that the oxygen is half used. This being so, the function of the catalase is easily understood. Through the action of this hydrogen-peroxide-splitting enzyme half of the oxygen of the hydrogen peroxide is liberated and can thus function as hydrogen acceptor once more. Thus the catalase is an enzyme which renders possible a more economical use of the oxygen. This theory—which does not exclude other explanations—harmonizes with the small content of catalase in such organisms as are adapted to life without oxygen.

The oxygen in the expired carbon dioxide does not originate from the oxygen in the atmosphere but comes from other sources.

Part of it comes from the oxygen which is originally a content of the molecules of the food stuffs and which remains in its combination with the carbon atoms of the carbonic chain, when the hydrogen atoms are split off by the dehydrogenases. Another part of the oxygen in the expired carbon dioxide is due to the water molecules added to the carbonic chain, particularly in those places where double bonds are formed by dehydrogenations as well as by the change of the aldehyde groups to aldehyde hydrates. It is, of course, quite possible that the water thus added comes from the water formed by the reaction between the oxygen of the atmosphere and the hydrogen of the food stuffs. But the water formed in this way is so small a fraction of the total water content of the organism that it is of no account.

In this connexion I should like to say a

few words about the usual reaction formula for the oxidation of a carbohydrate, e.g. glucose.

$$C_6H_{12}O_6 + 6\,O_2 = 6\,CO_2 + 6\,H_2O \qquad (1)$$

Naturally this formula is correct if it claims to show only the new products found in a reaction mixture where glucose is burned and to show the stochiometric relations between the substances in the formula. But if we want the reaction formula to give the *genetic* relation between the atoms on both sides of the equality mark in the equation, then the equation is unsatisfactory. It does not express the biological oxidation of the glucose, such as I have interpreted it. The formula must then be amplified and water must be introduced in the following way.

$$C_6H_{12}O_6 + 6\,H_2O + 6\,O_2 = 6\,CO_2 + 12\,H_2O \qquad (2)$$

The formula (1) can be criticised from the genetical point of view on the ground that six of the twelve atoms of oxygen which are denoted as forming part of the carbonic acid on the right side of the sign of equality do not come from the glucose but from a substance—water—which is not denoted in the formula. Consequently the formula is not to be looked upon as the result of an abbreviation due to the leaving-out of intermediate links—which, of course, is allowed—but is incorrect, in that it suggests a genetic relation which does not exist.

Formula 2 is faultless from this point of view but without further amplification it is of no great value. On this ground I have tried to explain it by putting in lines of connexion and arrows in order to make clear the genetic relations between the atom groups which are of interest here.

This opinion of mine that oxygen consumed by a certain oxidation process is changed to water and that the oxygen in the carbon dioxide comes from the oxidized substance or from the added water, is perhaps somewhat surprising. It is however supported by certain well-known processes from organic chemistry.

As early as 1886 Dixon showed that water probably participates in the usual oxidation process of carbon monoxide. In its dry form carbon monoxide reacts with oxygen only at very high temperatures. For the oxidation of carbon monoxide at the temperature of an ordinary flame the presence of water is absolutely necessary. The reaction which takes place under these conditions shows the following stages, as has been shown later by Wartenberg and Sieg.

$$(1) \qquad CO + H_2O = H.COOH$$
$$(2) \qquad H.COOH + O_2 = CO_2 + H_2O_2$$
$$(3) \qquad H_2O_2 = H_2O + O$$

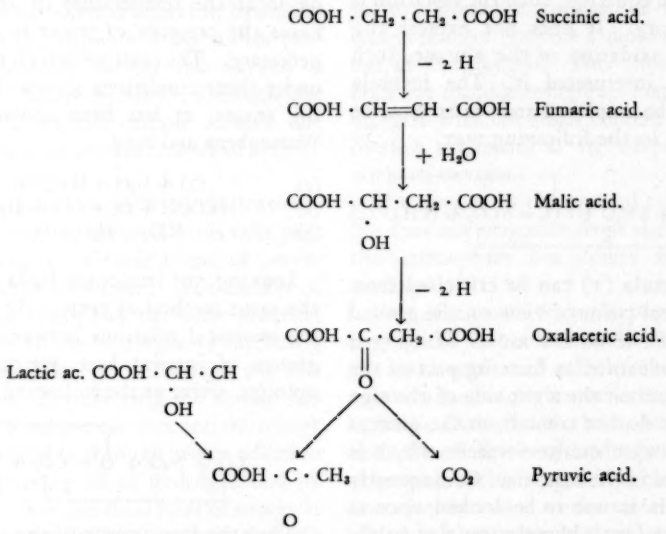
Leaving out irrelevant links and using the same method as previously for denoting genetical relations between the atom groups of interest here, we must, in my opinion, arrive at the following results:

$$CO + H_2O + O = CO_2 + H_2O$$

Thus the free oxygen of the atmosphere gives here also water as its final product. The oxygen in the carbon dioxide comes from the oxygen partly in the carbon monoxide, partly in the water.

With regard to this general conception of the final fate of the oxygen consumed it may be objected that it has not yet been proved. This is true but the objection applies even more to the older view. In support of the conception which I have outlined above it may be pointed out that, as far as experiments in this field are available, they harmonize well with my theory.

Of special value in this respect are the investigations carried out in Professor Otto Frank's laboratory in Munich. Professor Hahn, in collaboration with Haarmann and Fischbach, has investigated the reactive chain of which succinic acid is the first link. They have been able to establish the following series: succinic acid, fumaric acid, malic acid, oxalacetic acid, pyruvic acid. Nowhere in this chain occurs a direct attack of the oxygen on the carbon of the carbon chain.


COOH · CH₂ · CH₂ · COOH Succinic acid.
− 2 H
COOH · CH=CH · COOH Fumaric acid.
+ H₂O
COOH · CH · CH₂ · COOH Malic acid.
OH
− 2 H
COOH · C · CH₂ · COOH Oxalacetic acid.
O
Lactic ac. COOH · CH · CH
OH
COOH · C · CH₃
O
CO₂ Pyruvic acid.

I myself, in an earlier paper, pointed out that the oxidation of the salts of oxalic acid in the organism does not harmonize with the general view I hold concerning these things, because they do not contain any hydrogen. However, during my research on the dehydrogenases in seeds I had occasion to return to this question and I found that oxalic acid, also in the form of a neutral salt is subjected to a hydratation and that it is oxidized by dehydrogenation. Consequently the oxalic acid is in reality no exception to the general rule. My observations regarding the hydratation of oxalic acid harmonize very well with the views of Bôeseken, the well known Dutch chemist, about the real constitution of oxalic acid.

8. XANTHIN DEHYDROGENASE

To Sir F. G. Hopkins and collaborators in Cambridge is due the merit of discovering that the field of action of the dehydrogenases embraces also a class of substances of quite a different sort than those treated above.

In 1922 Hopkins, Morgan and Stewart published the observation that the enzyme roughly characterized for the first time in 1905 by Burian and called by him xanthin oxidase belongs in reality to the dehydrogenases.

This enzyme is present in the tissues of the body, but its extraction was attended with difficulties until the English scientists detected its presence in milk.

Thanks to the work of the Cambridge school we now have at our disposal methods for extracting it from the milk in a concentrated form and—as far as we are able to judge—free from other dehydrogenases, with the exception perhaps of the Schardinger enzyme.

The biological substrates of this enzyme are xanthin and hypoxanthin. These substances seem to exist, at least to a certain extent, in their hydrate forms. The xanthin dehydrogenase transforms them to uric acid by depriving them of certain hydrogen atoms. The investigations of this enzyme have further shown that the action of this dehydrogenase also is characterized by pronounced specificity. It seems to have a weak oxidising power on adenin and, among the substituted purines, on 6-8-dihydroxipurine and 2-thioxanthine, besides its normal effect on hypoxanthine and xanthine. If a methyl group is introduced into the pyrimidine or iminazole ring this is sufficient to prevent activation entirely.

Perhaps there exists one exception to this high degree of specificity. The enzyme preparates obtained hitherto are able also to activate aldehydes, and thus give the typical Schardinger reaction. It may be possible, though, that the xanthin dehydrogenase and the aldehyde dehydrogenase are different enzymes, but with physical characteristics so nearly identical that the two substances can be isolated only with difficulty.

In 1924 Dickson and Thurlow showed that certain purines, in spite of not being activated by the dehydrogenase, are absorbed on its surface. In this way they prevent the dehydrogenase from activating the hydrogen of xanthine and hypoxanthine. This makes a separate study possible on one hand of the absorption of certain substances on the enzyme and, on the other, of the activation of the substrate by the enzyme. If the Mb. is reduced, the purine substance must have been activated; if, on the other hand, the velocity of the reduction generally obtained by means of the xanthine is decreased when another purine substance is added, then an absorption of this other substance upon the enzyme must have taken place.

As pointed out by Sir F. G. Hopkins, the oxidation of xanthine and hypoxanthine to uric acid is a reaction which is difficult to obtain by the usual oxidising reagents. As a matter of fact, no one seems to have been able to do so. The explanation of this peculiar oxidation effect seems to be the same in the case of the xanthine substances as in that of succinic acid —viz. the activation of hydrogen.

9. THE DEHYDROGENASES OF BACTERIA

As pointed out in the introduction to this lecture the oxidation of alcohol to acetic acid by the acetic bacteria was one of the biological reactions on which Wieland founded his theory of biological dehydrogenation. But since then our knowledge of the bacteriological dehydrogenation processes has made great progress. This is due to the work of J. H. Quastel and his collaborators, Stephenson, Whetham, Woolf and Wooldridge, working in Sir F. G. Hopkins' Institute in Cambridge.

Quastel used the bacteria under such conditions that their growth during the experimental period was small or non-existant. In other words he used "non-proliferating" bacteria. With help of such bacteria he was able to study the simple katabolic processes without complication of the anabolic processes resulting in the formation of new cell substance. What he studied, using the non-proliferating bacteria, was then comparable to the metabolic processes in tissues from full grown higher organisms. Quastel calls the non-proliferating bacteria also "rest-

ing bacteria," regarding them as comparable with resting muscles and other tissues. I myself prefer not to use the name "resting" bacteria. The non-proliferating bacteria are, with regard to their metabolism, comparable with non-growing tissues, resting or non-resting, independent of their degree of activity.

The conditions, that growth shall be small or absent during the experimental time, are easily secured, if the experiments are carried out:

1. In the absence of some factor essential for growth, e.g. a nutritive source of nitrogen in the culture.

2. Anaerobically.

3. In a short time—usually under thirty minutes.

4. At a relatively high temperature (i.e. a temperature at which growth is known either to be inhibited or not to occur, but which does not seriously interfere with the reaction under investigation.)

Bacteria used under these conditions lend themselves to investigation in the same manner as enzymes or other catalytic systems, and it has been possible to show that the bacteria suspensions have many factors in common with enzyme systems. The easy manipulation of non-proliferating bacteria, and the fact that conditions can be well controlled, make it possible to obtain reproducible and consistent results.

Among the results arrived at by Quastel and his collaborators during the course of their experiments on *Bacillus coli* may here first be mentioned their discovery of a great number of organic substances activated by *B. coli*. Using the Mb. technique Quastel found that 56 substances could be activated, although these substances otherwise are quite inert, apart from the influence of living cells.

When drawing his conclusions from these observations Quastel makes a mistake, which, however, is a fortunate one. His mistake is that he credits me with the opinion that every activated substance requires each its absolutely specific enzyme. According to him my opinion would be that these 56 activated substances should require 56 specific enzymes.

Quastel is quite right in regarding this as highly improbable. Among the substances activated by *B. coli* are several which cannot be supposed to exist in the usual media. That the bacillus should have at its disposal specific enzymes for these substances can be excluded. As is evident from what has been said above, I have on the contrary distinctly repudiated the idea of absolutely specific enzymes. It is true that I hold a pluralistic view of this class of enzymes, but this does not mean that I believe in absolutely specific enzymes. Quastel's mistake, which he shares with other authors, is probably due to some unsatisfactory abstract of my original, difficultly accessible paper.

I said just now that Quastel's mistake was a fortunate one. It has led him to an interesting explanation—useful at least as a working hypothesis—of the mechanism by means of which the bacteria activate the hydrogen of the various substances.

According to him the dehydrogenations are primarily due to polarisations of substrate molecules induced by electrical fields which characterize particular centres —the "active centra"—of cellular and intracellular surfaces. If the polarisation is effective enough, the molecule may in that way become a hydrogen donator or acceptor.

In order to understand Quastel's conception of the active centra of the cells, it is perhaps best to start from an opposite and simple chemical view of the dehydrogenating enzymes. Let us thus consider them as protein molecules with a certain

group, specific for the enzyme character. We can call it the "prosthetic" group.

For Quastel the dehydrogenetic actions of the cells do not generally depend on such a simple molecule but on the existence of a certain structure, in other words on a complex of molecules forming a relatively stable physical aggregate. As is the case in many solid mechanical systems the structure of a living cell and especially of its surface also may be the seat of a certain strain between the constituting molecules. A local production of an external electric field then will take place with a polarisation effect on such substances, which through their constitution have access to the field. These substances are in other words activated.

This view of Quastel has formed a working hypothesis for a great number of investigations which have considerably widened our field of knowledge concerning the factors influencing the hydrogen activating powers of the bacteria.

An interesting result of these investigations was the establishing of the fact that the destructive action of different factors is highly selective. Under influence of a certain factor *B. coli* may lose its dehydrogenating power with regard to a certain substance without changing it regarding another. A step by step degradation occurs. Bacteria treated with ether or toluol lose their power to activate sugar, acetic, gluconic and glutamic acids, but keep unchanged their power to activate formic, lactic and succinic acid.

It seems very probable, that Quastel's ideas regarding the "active centra" are due to his working with bacteria. In these small organisms the surface is of comparatively more account than in bigger cells. The bacteria are scarcely anything more than a surface-membrane. The first and quite necessary function of a cell membrane is to prevent the dissolution of the cell in its fluid medium. Hence their stable structure.

In the case of such cells it is tempting to look upon the solid structure as essential for functions which in other cells are not necessarily bound to a structure.

If we work on larger cells and on tissues of softer consistency we are not so easily tempted to attach such a high importance to the cell structure for the dehydrogenation processes. No great change is found in the dehydrogenation processes if we place the cells in hypotonic fluids. The water which is then taken up must penetrate between the colloidal molecules and effectively change the existing intermolecular strain. Were this strain of great importance, the dehydrogenation would be much altered. From such cells it is also more easy to extract the dehydrogenases in soluble form. Here they show their power to work independent of a structure.

To go back to the step by step narrowing of the action field of the dehydrogenases under the influence of some destructive factor, it seems not to exclude even the simple assumption that the dehydrogenase influenced is a simple protein molecule with an active prosthetic group. As the various haemoglobins have different qualities and as the oxygen combining peculiarities of a certain haemoglobin can be changed by influencing its protein group, so the difference, due to factors influencing the protein component of the dehydrogenase-molecule, may be able to change the field of action of the enzyme.

10. THE DEHYDROGENASES IN SEEDS

A great number of seeds contain stores of dehydrogenases. In certain seeds they occur in such form that these seeds are the best material for the detection of dehydrogenases and for the study of their qualities.

If the resources of the Mb. technique

are available it is sufficient, in order to show certain dehydrogenation reactions, to place the necessary amount of Mb.-donator-solution and of pulverized seed in a vacuum tube. After the evacuation of the tube and the placing of it in a thermostat the decoloration characteristic of the dehydrogenases will soon occur. In many cases it is better to use a water solution or a salt solution of the seed instead of the pulverized seed. A neutral potassium phosphate solution is often particularly suitable.

Different seeds behave very differently during these experiments. Thus, seeds show great differences in the velocity of their "spontaneous decoloration," i.e. the decoloration of the reaction mixture under the conditions of the Mb. technique but without the addition of a special donator. This spontaneous decoloration as a rule is, e.g., considerably greater in the case of peas than of cucumber seed.

Naturally these enzymatic decoloration processes must be distinguished from others of non-enzymatic origin—not requiring dehydrogenases and hydrogen donators. Thus in my experiments with seeds from *Acacia lophanta* I found a particularly strong Mb. reduction, which however did *not* show the sensitiveness to temperatures above 60°C. characteristic of the dehydrogenases. When the pulverized seed was mixed with a phosphate solution a strong smell of onions appeared. It is tempting to connect the strong reduction effect with the presence of some reactive volatile substance.

When such substances which may possibly act as donators are added to the mixture in the tubes, the decoloration process varies in different seeds.

In many cases there is no effect on the Mb. even when a great many substances are tested. Obviously continued testing might lead to the discovery of some donator. It is possible also that with some other acceptor than Mb. one or the other of the tested substances would reveal itself as a donator. Very often the existing spontaneous decoloration and the lack of effect when some donator is specially added, may be due to the fact that the system already possesses donators in optimal amount. In such cases the addition of more donators has naturally no effect. Some kinds of seeds are, however, very sensitive to an addition of suitable donators.

Seeds which are at all sensitive to donators behave differently towards different donators. Experience has shown that certain substances will act as donators more often than others. Thus formic acid, malic acid, glutamic acid, hexosediphosphoric acid, and ethyl alcohol are active on a number of seeds, but the degree of their activating power varies. Malic acid may be more active than, e.g., alcohol in one case, but in the case of another seed the conditions may be reversed.

It is a rather remarkable fact that I have found no trace of activating power on seeds in the case of succinic acid, which is such a strong activator where animal tissues are concerned. Once I thought I observed such an effect in the case of succinic acid, but it turned out to be due to the effect of malic acid present in the succinic acid preparate.

As a rule the seeds used have been very slightly sensitive to simple or compound carbohydrates. But they are all the more sensitive to the addition of hexosediphosphoric acid—but not to hexosemonophosphoric acid. Perhaps the strong effect of the hexosediphosphoric acid is due to the change of the carbohydrate molecule into a polyvalent ion. Probably the high electric charge of such an ion brings about

quite different conditions of adsorption than those existing in the case of the neutral molecule.

A point which must always be considered during these researches is the following: Is the substance with apparent donator effect a real donator, or does it obtain this power only after some change or other?

The results mentioned above are most easily interpreted from a pluralistic view of the dehydrogenases. Probably seeds possess a series of dehydrogenases, each with a limited field of action. Different seeds may possess the same or different dehydrogenases.

The question of the degree of specificity of each enzyme may be left open. I consider it possible that enzymes may possess different degrees of specificity in different seeds. I have found, e.g., some seeds which are strongly activated by ethyl alcohol but not at all by propyl alcohol. Other kinds of seeds are activated by ethyl alcohol as well as by propyl alcohol, though the effect is less strong in the case of the latter substance.

It is possible that in the case of this seed there are two enzymes, one for ethyl alcohol and one for the propyl alcohol. Perhaps the enzyme in the latter case is less specific.

The hypothesis that different seeds possess different specific enzymes is supported by the fact that some seeds are activated by substances which lack every trace of activating power in the case of most seeds.

Citric acid, e.g., behaves as a particularly effective activator in the case of cucumber seeds, while I have observed no effect of this acid on the other seeds, which I have investigated (with the exception perhaps of *Malva* seed). Oxalic acid shows a clear if not a specially strong activating power in the case of seeds of some species of *Malva* and, perhaps, of two other plants also. But as a rule citric acid as well as oxalic acid are not only incapable of hastening the enzymatic decoloration process of seed extracts, they even retard it in many cases.

Similar effects of inhibition are not unusual when substances chemically rather inactive are added. The inhibition is probably caused by the adsorption of these substances on the surfaces of the dehydrogenases, although these substances are not activated. By this adsorption the inhibiting substances cause the real donators to be removed from the activating surfaces.

Thus we discover in the case of the dehydrogenases of seeds the same effects which have been studied with such great success by Dixon and Thurlow in the cases of the xanthine dehydrogenase and by Quastel and collaborators in the case of bacteria.

11. THE DEHYDROGENASES OF POLLEN

In order to understand the function of the dehydrogenases it is necessary to investigate as many types of cells as possible; above all, no cell type with a distinctly specific function must be left out of consideration.

I have therefore included in my investigation also the sex cells. Up till now I have only had time to investigate the pollen of hazel (*Corylus avelana*). It was easy to show the existence of dehydrogenases in these cells. The dehydrogenases found were able to activate malic acid, glycerophosphoric acid, and certain alcohols, especially ethyl alcohol, propyl alcohol and normal butyl alcohol.

12. SOME FURTHER REMARKS ABOUT THE SPECIFICITY OF THE DEHYDROGENASES

When in my earliest papers I expressed a pluralistic view of the nature of the dehydrogenases, I based my opinion on the observation that it was possible to obtain

a succino-dehydrogenase preparation with powerful action on succinic acid but without power to activate the great number of other metabolites investigated by me. Further investigation has revealed the fact that the dehydrogenase preparation which I used is able to activate also glycerin-phosphoric acid and hexosediphosphoric acid. But this does not necessarily point to the assumption that these substances are activated by the succino-dehydrogenase itself. The simplest and most likely explanation is that the succino-dehydrogenase preparation contains also one or more other dehydrogenases. I leave it an open question whether the glycerin-phosphoric acid and the hexosediphosphoric acid are activated by the same dehydrogenase or by different ones. The fact that the succino-dehydrogenase does not influence these substances is evident, since it is possible to obtain from seeds preparations which have a very strong activating influence on hexosediphosphoric acid and a noticeable influence on glycerin-phosphoric acid but none whatever on succinic acid.

It has been objected that the dehydrogenase preparations made according to the method which has been described by Andersson from my laboratory, do not show the specificity which, according to what has been said above, ought to characterize the succino-dehydrogenase. They will activate also, e.g, lactic acid. However the preparation according to the method described by Andersson is not intended to show the highest degree of specificity. The aim of this method is only to obtain in an easy way a succino-dehydrogenase preparation which will show the characteristic effect of this enzyme on succinic acid. If a preparation of the highest possible specificity is required, the material used must be subjected to a much more effective washing.

A good evidence for the specificity of the succino-dehydrogenase is also the fact that the lens substance of the eye activates lactic acid, malic acid, citric acid, and glycerin-phosphoric acid, but has no power to activate succinic acid, as shown by Ahlgren.

The investigations from the laboratory of Sir F. G. Hopkins also point to a high specificity of the xanthin-dehydrogenase. And this same laboratory has lately furnished further proofs for the truth of the theory of the high specificity of the dehydrogenases. Thus Miss Marjory Stephenson has succeeded in obtaining from *Bacillus coli* a specific soluble lactico-dehydrogenase. *Bacillus coli* was cultivated on a suitable substrate containing sodium lactate and, after being thoroughly washed, was left to autolyse for a number of days in a phosphate solution and then centrifuged. The clear supernatant liquid was found to contain a lactico-dehydrogenase with a small power to activate also α-hydroxybutyrate. Further, Bernheim has been able to extract a soluble citrico-dehydrogenase free from other tissue-dehydrogenases. He used fresh liver substance from oxen, sheep and pigs, which substance, after being minced, was dehydrated by acetone, and when the dry liver powder was extracted with water this solution contained only citrico-dehydrogenase but no other dehydrogenase. But if the solution is made with di-sodium phosphate, both xanthine-dehydrogenase and succino-dehydrogenase are found in the solution.

Bernheim has also been able to obtain a lactico-dehydrogenase in soluble form and free from other dehydrogenases by extracting acetone-dry yeast with phosphate solution for a short period. If the extraction is carried on too long, the succino-dehydrogenase also is extracted. The lactico-dehydrogenase obtained has also a certain power to activate α-oxybutyric acid.

13. THE BEHAVIOR TOWARDS OXYGEN OF THE HYDROGEN ACTIVATED BY THE DEHYDROGENASES

The salient point of the oxidation theory of Wieland is, in my opinion, the view that the oxidation of the dysoxidisable substances is made possible by the activation of their hydrogen. Wieland finds no reason to assume also an activation of oxygen for the oxidation processes he has studied. In his opinion the hydrogen activated by the catalyser can react with the unchanged inactive oxygen. For the oxidation processes investigated by me I have on the whole accepted Wieland's theory. However, during my earliest experiments I made an observation, which was difficult to explain without assuming a certain activation of the oxygen also. As is known from the investigations of Battelli and Stern, KCN inhibits very effectively the enzymatic oxidation of succinic acid in an O_2-medium. Investigating the effect of KCN on the oxidation of succinic acid in vacuo in the presence of Mb., I found that this process was not inhibited by KCN. This last very peculiar fact led me to conclude that KCN does not affect the succino-dehydrogenase. In order to explain the inhibitive effect of KCN, which in spite of the insensitivity of the dehydrogenase for KCN was observed in the first case, I formed a hypothesis based on the assumption that a certain activation of oxygen is also necessary for this reaction between hydrogen and oxygen. On the basis of the views of the kinetic gas theory I felt entitled to conclude that of the oxygen present in the reaction-mixture a small part occurs in an activated form due to the collision of the molecules. It is this "spontaneously activated" part of the oxygen which, in my opinion, was able to serve as acceptor for the activated hydrogen in my experiments. On the other hand, this small part, to the extent it does occur, is being continuously inactivated, when KCN is present.

The facts under discussion here have also been explained in other ways. In 1928 Wieland and Bertho launched the explanation that through its adsorption on the dehydrogenases Mb. has the power to expel the KCN from these enzymes and thus prevent its effect.

The question whether hydrogen activated by the dehydrogenases is accepted by unactivated oxygen has been further illustrated by certain new observations.

Certain dehydrogenase solutions do not react with the oxygen of the atmosphere, although they react with Mb. But this distinction does not exist in the case of the dehydrogenases still bound to the cells. Miss Marjory Stephenson has thus found that the lactic acid dehydrogenase still bound to the bacteria can transport the hydrogen to the oxygen of the atmosphere. If, on the other hand, this dehydrogenase is brought into solution, it loses this power but is still able to reduce Mb. Bernheim has reached a similar result in the case of the dehydrogenase of liver substance and of the lactico-dehydrogenase from the tissues of the higher animals.

In the case of the succino-dehydrogenase and the xanthino-dehydrogenase the observations of different investigators contradict each other. In the laboratory at Lund we have worked with succino-dehydrogenase solutions which were still able to use the oxygen of the atmosphere. Von Euler has published the observation that succino-dehydrogenase solutions often lack this power, while not only some but all of the solutions prepared by Miss Stern are recorded to be ineffective in this respect. Regarded in connection with the generally accepted fact that, so long as they are bound to the cell substance, the dehydrogenases have in every case the

power to use the oxygen of the atmosphere, the observations of Stephenson, Bernheim and others point to the presence in the cells and tissues of an insoluble factor or of a factor which is dissolved only with difficulty or as an emulsion, a factor which must be responsible for the reaction between the activated hydrogen and the oxygen.

On this point the excellent investigations of Keilin have a great significance. Keilin has found that cells of aerobic organisms contain a respiratory pigment, cytochrome, and also a real oxidase, which he calls the indophenol oxidase. These two substances collaborate in the following way. The indephenol oxidase is able to transfer oxygen to the cytochrome and thus to change it to its oxidized form. It is this oxidized cytochrome which in its turn has the power of reacting with the hydrogen activated by the dehydrogenases. The cytochrome-indophenol-oxidase system seems difficult to extract and bring in the form of a solution. In the still intact cells and tissues the dehydrogenases collaborate with this system and are thus able to use the oxygen of the atmosphere. Solutions of dehydrogenases, on the other hand, lack the cytochrome system and are scarcely able to use the oxygen.

Keilin has shown that the indophenol oxidase is rendered inactive by KCN, while this substance does not affect the dehydrogenases. Thus the difference between the action of KCN on the O-oxidation and on the Mb.-oxidation is explained in a very interesting way.

14. FURTHER FUNCTIONS OF THE DEHYDROGENASES

In describing the dehydrogenases Wieland realized that a series of different effects must be ascribed to this new group of enzymes. In transporting hydrogen from the donator substance to the acceptor substance the dehydrogenase acts both as an oxidase and a reductase. This means that the assumption of the existence of special reductases must be given up. Wieland pointed out that these enzymes can also transfer hydrogen from one molecule to another of the same substance. Thus two molecules of an aldehyde can be brought to react with one another in such a way that the one molecule is changed to the corresponding alcohol and the other to the corresponding acid. In this way is brought about what is termed a mutase effect or a "disproportionation" (in German "*Disproportionierung*"). That is to say, what have hitherto been called "mutases" are in reality dehydrogenases. The biological Cannizzaro-reactions hitherto observed may be said to be due to dehydrogenases.

When I first began my investigations in this field I suggested that this enzyme group may also be able to carry out syntheses of short carbon chains to longer ones. Having observed the enzymatic dehydrogenation of acetic acid and having found it difficult to explain in any other way, I formed the hypothesis that two molecules of acetic acid giving off two hydrogen atoms are linked together to form one molecule of succinic acid. This hypothesis has played a part in the discussion of the routes of the intermediate metabolism, and given rise to special investigations. It has been possible to bring about this synthesis in model experiments in vitro without the help of enzymes and certain bacteria are also able to perform it. But up to now its presence in the tissues of the higher organisms has not been proved. This may possibly be due to a difficulty in finding the suitable hydrogen acceptor and in preventing the simultaneous transformation of the succinic acid eventually formed.

This enzyme group is of special interest

also on account of the reversible processes to which it gives rise.

When succinic acid is being transformed to fumaric acid under the influence of the succino-dehydrogenase, there takes place at the same time and under the influence of the same enzyme a transformation of fumaric acid to succinic acid. The quantitative relation between the two contrary processes depends on the relative amounts of the two substances.

That is to say: the succino-dehydrogenase is at the same time a fumarico-hydrogenase. Such considerations as this seem to excuse the name "hydrogeno-transportase" which I have allowed myself to give to this enzyme group.

The first to investigate the reversible processes just referred to were Quastel, Stephenson and Whetham. They used *B. coli*. Later I myself, using the succino-dehydrogenase of muscle substance, studied the equilibrium between succinic acid and fumaric acid.

The oxidation-reduction processes or, if you do not object to this short form, the redox processes carried out by the dehydrogenases may be measured by electrical methods.

For the history of the electric potentials due to the redox processes of living cells or of biological enzyme systems I refer my audience to the excellent works of Clark, Needham and Needham, and Michaelis.

15. THE USE OF THE Mb. TECHNIQUE IN QUALITATIVE AND QUANTITATIVE ANALYSIS

It is clear from what has been said above that the reduction of Mb. in vacuo requires the presence of a donator substance as well as of the corresponding specific enzyme. The Mb. reduction does not take place when one or the other of these factors is lacking. Mb. + succinic acid give no reduction, nor Mb. + succino-dehydrogenase. If, on the other hand, the system is made complete so that all the three substances: Mb., succino-dehydrogenase, and succinic acid, are present, then the reduction is certain.

This fact enables us to use the enzymatic decoloration in question in the service of biochemical analysis. If we add a substance of unknown composition to a solution of Mb. and succino-dehydrogenase and no decoloration follows, it is a fairly safe conclusion that the unknown substance contains no succinic acid. But, when the result is a decoloration there is reason to suppose that the unknown substance contains succinic acid.

The question to what extent the reduction caused by an unknown substance in the system Mb. + dehydrogenase makes the presence of succinic acid probable or certain, is intimately bound up with another: viz. that of the specificity of the succino-dehydrogenase solution employed.

Were it possible to use a pure succino-dehydrogenase free from all other dehydrogenases and if the succino-dehydrogenase could be considered as being absolutely specific, then the appearance of an enzymatic decoloration when an unknown substance is added would be a certain evidence for a content of succinic acid in the substance employed.

However, neither of these two assumptions is fully realized. At present it is impossible to obtain a chemically pure solution of succino-dehydrogenase. But this is of minor account. A more important fact is that all succino-dehydrogenase solutions have been found to contain other dehydrogenases also. In addition they contain an enzyme active on glycerinphosphoric acid. Lately it has been found that the succino-dehydrogenase solution made from muscle substance in the usual way is able to activate also hexose-diphosphoric acid.

Even if we should succeed in obtaining a succino-dehydrogenase solution free from other dehydrogenases, we should not be entitled to attribute to it an absolute specificity. Besides succinic acid the dehydrogenase seems to activate also methyl-succinic acid.

But although these circumstances influence the certainty of this analytic method, they do not invalidate it altogether. But they make certain precautions necessary. If, then, an unknown substance added to a solution of Mb. and succino-dehydrogenase will cause decoloration, special experiments are necessary in order to show whether the decoloration is due to succinic acid, to glycerin-phosphoric acid, or to hexose-diphosphoric acid. The fact that in order to cause a decoloration the glycerin-phosphoric acid must be much more concentrated than succinic acid, enables us often to exclude the possibility of glycerin-phosphoric acid. If, then, a very small amount of a substance will cause decoloration, it is very improbable that the glycerin-phosphoric acid is the responsible factor.

In order to find out whether a decoloration process is due to the succinic acid or to the hexose-diphosphoric acid, it is possible to use another dehydrogenase system. From certain seeds we are able to obtain dehydrogenases activating hexose-diphosphoric acid which have no influence on succinic acid. If an unknown substance causes reduction of the Mb. succino-dehydrogenase system obtained from muscle substance but has no effect on the dehydrogenase system from seeds it must contain succinic acid and cannot contain hexose-diphosphoric acid.

In 1917, before we knew that the succinic dehydrogenase preparations contain also dehydrogenases activating glycerin-phosphoric acid and hexose-diphosphoric acid, I made some experiments with the method just described in order to detect a possible content of succinic acid in animal tissues and fluids.

A great advantage with this method is its sensitiveness. Factors in this sensitiveness are (1) the relation between the molecular weights of succinic acid and Mb., respectively, and (2) the lowest concentration, in which Mb. can still give a solution showing appreciable color.

The value of the molecular weight of the succinic acid can be put at 118.1 and the same value for Mb. at 336.4. Since one molecule of succinic acid is sufficient to change one molecule Mb. to its leuco-form, one part succinic acid is sufficient to decolorize three parts Mb.

Regarding the question, what is the least amount of Mb. still detectable in water, it may be said that it is still possible to detect the blue color of one cc. of Mb. solution at a dilution of 1:1000000. One cc. of such solution contains only 0.001 mgm. Mb.,—i.e. one microgram (= 1γ). This amount of Mb. requires for decoloration only 0.33 microgram of succinic acid. Theoretically it would be possible to detect even this small amount of succinic acid with the help of the Mb.-dehydrogenase method. In my practical work I found it advisable to limit the sensitiveness of the method to 20 micrograms of succinic acid.

During experiments with this method I met some difficulties when trying to extract the small amounts of succinic acid present in the tissues. The experiments were for this cause postponed. But during the ten years which have elapsed since these experiments were first begun I have never given up the idea of using the Mb.-dehydrogenase systems for analytical work and about a year ago I succeeded in finding a Mb.-dehydrogenase system which seems to make possible the determination of citric acid in animal tissues

and fluids in very small amounts not detectable with other technical methods.

The technique is based on the presence in cucumber seeds of a dehydrogenase with the power to activate citric acid. When a perfectly fresh phosphate solution of cucumber seeds of a convenient sort, to which Mb. has been added, is investigated by means of the Mb. technique, its spontaneous decoloration will be found to be very small. The fact that the decoloration is small is not due to the absence of active enzymes but obviously to the small quantity of donator substances. This is proved by the fact that the velocity of the decoloration process is considerably increased when certain hydrogen donators are added. The dehydrogenases in the cucumber seed extract were obviously in need of donators. The most important donators for this extract are malic acid, ethyl alcohol, glycogen, dextrin, hexosediphosphoric acid, and citric acid. Citric acid and hexosediphosphoric acid form a group by themselves on account of their capacity of serving as donators for the dehydrogenases of the cucumber seeds. Only very small quantities of these substances are necessary in order to reach the maximal velocity of decoloration which is ever obtainable with these substances. As regards the effect of citric acid and malic acid, it is possible to obtain with both these substances the same high decoloration velocity but in order to achieve this result we must use 250 times as much malic acid as citric acid. As has been pointed out in another connection, malic acid, ethyl alcohol and hexosediphosphoric acid are among the most common of all donators for seeds. But with citric acid the case is quite different. Among the great number of seeds investigated in this respect I have found citric acid active as donator only in the case of seeds from cucumber and from *Malva crispa*, but in the latter case the action was weak.

The discovery of this peculiar reaction of cucumber seeds to citric acid made me ask: Is it possible to base on this fact a method for detecting even small amounts of citric acid in animal tissues and fluids?

Somebody may ask: Is there really need for such a method?

I myself do not hesitate to answer in the affirmative. Having detected, in 1909, the great oxidizing power of animal tissues with regard to citric acid, and, in 1918, the citrico-dehydrogenase, I have since considered it highly probable that citric acid is a normal intermediate product in metabolism. I have ventured the guess that it might be possible to detect citric acid in many animal fluids and tissues, if only methods sufficiently sensitive were at our disposal. Now it seemed possible to make use of this peculiar behavior of cucumber seeds with regard to citric acid in order to detect even small amounts of this substance.

It ought to be mentioned that in 1891 Henkel had detected the presence of citric acid in milk. Further experiments of Amberg, McClure, Mayer, and Woods have shown that citric acid is present also in urine and sweat.

However, the methods used by these investigators are far from possessing the sensitiveness and rapidity of the dehydrogenase method. It is this lack of suitable methods which in all probability has caused the noticeable scarcity, up to now, of investigations concerning the citric acid content in animal fluids and tissues.

The careful investigations of the behavior of cucumber seed extract to Mb. in vacuum which have been carried out at the Physiological Institute of Lund, have shown that if very small amounts of a certain solution have already the power of increasing tenfold the decoloration velocity of Mb., it is in reality out of the question to ascribe this action to any other substances but citric acid or hexose-diphos-

phoric acid. In order to decide to which of these two substances the effect in question is due, it is possible to build on the fact that many seeds react strongly to hexose-diphosphoric acid but not at all to citric acid. Seeds from, e.g., *Citrus aurantium dulcis* (orange) and from *Corchorus capsularis* (jute) behave in this way.

By making use of this relation of cucumber seed extract to citric acid it has been possible to create also a quantitative method for the determination of citric acid in animal fluids. A fact of special importance for this method is that we are able to decide accurately the minimal quantity of citric acid required for the maximal velocity of the decoloration process. If we go below this minimal quantity the decoloration velocity decreases very rapidly. The method is the more convenient and easy since it is unnecessary to extract and isolate the citric acid from the animal fluids. The activity of the cucumber seed enzyme is not—or is only in a small degree—affected by the other components of the animal fluids. With regard to the practical use of the method I will confine myself to a few points. Equal amounts of cucumber seed extract are placed in two series of vacuum tubes. Increasing quantities of a citric acid solution of convenient concentration are added to the one series. To the vacuum tubes of the other series are added increasing quantities of the fluid under investigation. Both series are treated in the way typical of the Mb. technique. By means of the first series we find the minimal quantity of citric acid giving the shortest decoloration time. The second series of tubes will show whether it is at all possible to reach the same short decoloration time with the fluid to be investigated and, if so, what quantity is needed. This series will also show whether the decoloration time can be shortened still more, if we add larger doses of the fluid. If this is the case the effect cannot be due to citric acid only but some other factor must be at work also. We are entitled to assume the existence in the minimal quantity of fluid required for the decoloration an amount of citric acid equal to that required for the same effect when the acid is added to the pure cucumber seed extract. Special experiments ought to be made from time to time with a view to testing whether an extra quantity of citric acid added to the fluid under investigation can be detected with a sufficient degree of accuracy.

A method must be valued according to the results achieved. What new discoveries have then been made by means of the method just described?

I give here a table showing the citric acid content of some animal fluids. All values are expressed in parts per thousand ("per mille").

ANIMAL FLUID	CITRIC ACID CONTENT IN PARTS PER THOUSAND	INVESTIGATOR
Urine	0.25–1.8	Östberg
Citric acid is never absent in urine from healthy people. It may go down to zero in nephritis		
Women's milk contains no citric acid before two days after delivery. The citric acid content then increases rapidly to 1.5		Jerlov
Cerebrospinal fluid	0.05–0.06	Benni
Fluid from epididymis of rabbit	2.5	Scherstén
Fluid from seminal vesicles of rabbit	1.5	Scherstén
Fluid from seminal vesicles of pig	6	Scherstén
Sperm of man	1.8–4.1	Scherstén
Sweat	About 0.1	Scherstén
Blood serum of man	Less than determinable	Östberg

With methods similar to that here described other metabolites are being investigated.

LIST OF LITERATURE

1. WIELAND AND COLLABORATORS

WIELAND, HEINRICH. Zur Verbrennung des Kohlenoxyds. Ber. d. Dtsch. Chem. Ges., Jg. 45, 1912.

———. Über Hydrierung und Dehydrierung. Ber. d. Dtsch. Chem. Ges., Jg. 45, 1912.

———. Über die katalytische Umwandlung von Schwefeldioxyd in Schwefelsäure. Ber. d. Dtsch. Chem. Ges., Jg. 45, 1912.

———. Einige Bemerkungen über die Hydrierung aromatischer Verbindungen. Ber. d. Dtsch. Chem. Ges., Jg. 45, 1912.

———. Studien über den Mechanismus der Oxydationsvorgänge. Ber. d. Dtsch. Chem. Ges., Jg. 45, 1912.

———. Über den Mechanismus der Oxydationsvorgänge. Ber. d. Dtsch. Chem. Ges., Jg. 46, 1913.

———. Über den Mechanismus der Oxydationsvorgänge (III). Ber. d. Dtsch. Chem. Ges., Jg. 47, 1914.

———. Über den Mechanismus der Oxydationsvorgänge (IV). Ber. d. Dtsch. Chem. Ges., Jg. 54, 1921.

WIELAND, HEINRICH, and AUGUST WINGLER. Zur Oxydation der Aldehyde. (Über den Mechanismus der Oxydationsvorgänge. V.) Liebigs Annalen, Bd. 431, 1923.

WIELAND, HEINRICH. Über den Mechanismus der Oxydationsvorgänge. VI. Liebigs Annalen, Bd. 434, 1923.

WIELAND, HEINRICH, and HERMAN LÖVENSKIOLD. Zur Reaktionsweise des Hydroperoxyds. (Über den Mechanismus der Oxydationsvorgänge, VII.) Liebigs Annalen, Bd. 436, 1924.

WIELAND, HEINRICH, and HELENE RAU. Über die Spaltung des Di-oxyäthylperoxyds durch Alkalien. (Über den Mechanismus der Oxydationsvorgänge. VII.) Liebigs Annalen, Bd. 436, 1924.

WIELAND, HEINRICH, and AUGUST WINGLER. Die katalytische Spaltung und Oxydation von Ketosäuren. (Über den Mechanismus der Oxydationsvorgänge, VII.) Liebigs Annalen, Bd. 436, 1924.

WIELAND, HEINRICH, and FRANZ BERGEL. Zum oxydativen Abbau der Aminosäuren. (Über den Mechanismus der Oxydationsvorgänge. VIII.) Liebigs Annalen, Bd. 439, 1924.

WIELAND, HEINRICH. Über den Mechanismus der Oxydationsvorgänge. IX. Liebigs Annalen, Bd. 445, 1925.

WIELAND, HEINRICH, and F. GOTTWALT FISCHER. Die Oxydationswirkung der Jodsäure und ihre Hemmung. (Über den Mechanismus der Oxydationsvorgänge, X.) Ber. d. Dtsch. Chem. Ges., Jg. 59, 1926.

WIELAND, HEINRICH, and F. GOTTWALT FISCHER. Zur Frage der katalytischen Dehydrierung. (Über den Mechanismus der Oxydationsvorgänge, XI.) Ber. d. Dtsch. Chem. Ges., Jg. 59, 1926.

WIELAND, HEINRICH, and WILHELM FRANKE. Die Aktivierung des Hydroperoxyds durch Eisen. (Über den Mechanismus der Oxydationsvorgänge. XII.) Liebigs Annalen, Bd. 457, 1927.

WIELAND, HEINRICH, and HERMANN SUTTER. Einiges über Oxydasen und Peroxydasen. (Über den Mechanismus der Oxydationsvorgänge. XIII.) Ber. d. Dtsch. Chem. Ges., Jg. 61, 1928.

WIELAND, HEINRICH, and ALFRED BERTHO. Das Wesen der Essigsäure-Gärung. (Über den Mechanismus der Oxydationsvorgänge. XV.) Liebigs Annalen, Bd. 467, 1928.

WIELAND, HEINRICH. Über den Verlauf der Oxydationsvorgänge. Ber. d. dtsch. chem. Ges., Jg. 55, 1922.

———. Über den Mechanismus der Oxydationsvorgänge. Ergebn. d. Physiol., Bd. 20, 1922.

———. Mechanismus der Oxydation und Reduktion in der lebenden Substanz. Handbuch der Biochem., 2. Aufl., Bd. 11, 1923.

———. Über den Verlauf der Oxydationsvorgänge. Schweiz. med. Wochenschr., Jg. 53, 1923.

2. THUNBERG AND COLLABORATORS

AHLGREN, GUNNAR. Über die spontanreduzierende Einwirkung der Muskulatur auf Methylenblau. Skand. Arch. f. Physiol., Bd. 41, Jg. 1921.

———. Contribution à la question de la spécificité des déshydrogénases. Compt. rendus, T. 87, 1922.

———. Gibt es einen Stoffwechsel in der Kristallinse? Skand. Arch. f. Physiol., Bd. 44, 1923.

———. Experiments on the respiration of malignant tissues. Brit. Journ. of Exper. Pathol., Vol. 4, 1923.

———. Sur le champ d'action des déhydrogénases musculaires. Acta medica scandin., Vol. 57, 1923.

———. Zur Kenntnis der tierischen Gewebsoxydation. Supplementbd., Skand. Arch. f. Physiol., 1925.

———. On the oxidation mechanism of the crystalline lens. Acta Ophthalmologica, Vol. 5, 1927.

ALWALL, NILS. Zur Kenntnis der enzymatischen Bildung von l-Apfelsäure aus Fumarsäure. Skand. Arch. f. Physiol., Bd. 55, 1929.

ANDERSSON, NILS. Zur Kenntnis der Herstellung der

Succinodehydrogenase. Skand. Arch. f. Physiol., Bd. 52, 1927.

COLLETT, MARY. The specificity of the intracellular dehydrogenases in frog's muscle. Journ. of Biol. Chem., Vol. 58, 1924.

ESSEN-MÖLLER, ERIK. Über den Einfluss einiger Chinderivate auf die Tätigkeit der Dehydrogenasen der Skelettmuskulatur. Skand. Arch. f. Physiol., Bd. 48, 1926.

———. Studien über die Einwirkung der Wasserstoffionenkonzentration auf die Oxydationsprozesse der Muskulatur. Skand. Arch. f. Physiol., Bd. 47, 1926.

EULER, U. v. Über die Beeinflussung der Gewebsoxydation sowie einiger ihrer Teilvorgänge durch Tetrahydro-naphtylamin. Skand. Arch. f. Physiol., Bd. 51, 1927.

GRÖNVALL, HERMAN. Untersuchungen über die Einwirkung einiger einfacher Narkotika auf die Succinodehydrogenase. Skand. Arch. f. Physiol., Bd. 44, 1923.

HENRIKSSON, ANTON. Zur Kenntnis der Kryolabilität der Gewebsoxydation. Skand. Arch. f. Physiol., Bd. 47, 1925.

KRESTOWNIKOFF, A. Die Wirkung des Lichtes auf den Entfärbungsverlauf in einem Dehydrogenase-Methylenblausystem. Skand. Arch. f. Physiol., Bd. 52, 1927.

LEHMANN, J. Über das Verhalten der Muskulatur verschiedener Tiere gegenüber d-Weinsäure bzw. l-Weinsäure. Skand. Arch. f. Physiol., Bd. 42, 1922.

MÅHLÉN, SVEN. Untersuchungen über die Einwirkung der Benzoesäure und der drei isomeren Oxybenzoesäuren auf die Succinodehydrogenase. Skand. Arch. f. Physiol., Bd. 53, 1928.

OHLSSON, E. Die Abhängigkeit der Wirkung der Succinodehydrogenase von der Wasserstoffionenkonzentration. Skand. Arch. f. Physiol., Bd. 41, 1921.

ROSLING, EYVIND. Untersuchungen über Muskelenzyme. Skand. Arch. f. Physiol., Bd. 45, 1924.

———. Om den Wieland' ske Dehydrringsteori og dens Anvendelse paa deo biologiske Forbraendingsprocesser. Hospitalstidende, Arg. 1924.

———. L'hormone pancréatique comme activateur de certaines enzymes des muscles. Compt. rend. d. l. Société de Biologie, Bd. 88, 1923.

SAHLIN, BO. Untersuchungen über den Einfluss einiger Kaliumsalze auf die Succinodehydrogenase. Skand. Arch. f. Physiol., Bd. 46, 1924.

SVENSSON, DAN. Über die Einwirkung der wichtigsten Urethane und einiger anderer Stoffe auf die Succinodehydrogenase. Skand. Arch. f. Physiol., Bd. 44, 1923.

THUNBERG, TORSTEN. Über die vitale Dehydrierung der Bernsteinsäure bei Abwesenheit von Sauerstoff. Zentralbl. f. Physiol., Bd. 31, 1916.

———. Zur Kenntnis der Einwirkung tierischer Gewebe auf Methylenblau. Skand. Arch. f. Physiol., Bd. 35, 1917.

———. En biologisk färgreaktion å bernstensyra. Sv. Läk.-Sällsk. Handl., Bd. 43, 1917.

———. Zur Kenntnis des intermediären Stoffwechsels und der dabei wirksamen Enzyme. Skand. Arch. f. Physiol., Bd. 40, 1920.

———. Sur la présence de certains ferments oxydants dans les grains de Phaseolus vulgaris. Arch. internat. de Physiol., Vol. 18, 1921.

———. Zur Frage des wasserstoffaktivierenden Vermögens der Zellen. Arch. Néerland. de Physiol., Vol. 7, 1922.

———. Zur Kenntnis der Stoffwechselenzyme der Nervenfasern. Skand. Arch. f. Physiol., Bd. 43, 1923.

———. Zur Kenntnis der Dehydrogenasen der Geschlechtszellen. Skand. Arch. f. Physiol., Bd. 46, 1925.

———. Das Reduktions-Oxydationspotential eines Gemisches von Succinat-Fumarat. Verhandl. d. l. Nord. Kongr. f. Physiol. u. Exp. Med. in Lund, Skand. Arch. f. Physiol., Vol. 46, 1925.

———. Zur Kenntnis der enzymatischen Oxydation der Oxalsäure durch Pflanzensamen. Zugleich ein Beitrag zur Kenntnis der Konstitution der Oxalsäure. Skand. Arch. f. Physiol., Bd. 54, 1928.

———. Acceptormethode, Dehydrasen der Carbonsäuren, Redoxpotentiale. Oppenheimer-Pincussen, Die Fermenten und ihre Wirkungen, Bd. 3, 1928.

———. Über das Vorkommen einer Citrico-Dehydrogenase in Gurkensamen und ihre Verwertung für eine hochempfindliche biologische Farbenreaktion auf Citronensäure. Biochem. Zeitschr., Bd. 206, 1929.

WIDMARK, E. M. P. Studien über die Succinodehydrogenase. Skand. Arch. f. Physiol., Bd. 41, 1921.

WISHART, GEORGE MACFEAT. On the reduction of methylene blue by tissue extracts. Biochem. Journ., Vol. 17, 1923.

3. F. G. HOPKINS AND COLLABORATORS

HOPKINS, F. G. Some oxidation mechanisms of the cell. Bull. Johns Hopkins Hosp., Vol. 32, 1921.

HOPKINS, F. G., E. J. MORGAN, and C. P. STEWART. Anaerobic and aerobic oxidation of xanthine and hypoxanthine by tissues and by milk. Proc. Roy. Soc., Vol. 94, 1922.

HOPKINS, F. G. Les mécanismes de l'oxydation dans l'organisme vivant. Bulletin de la Soc. de Chimie Biol., Vol. 5, 1923.

———. On current views concerning the mechanisms of biological oxidation. Skand. Arch. f. Physiol., Bd. 49, 1926.

DIXON, M., and SYLVA THURLOW. Studies on xanthine oxidase II. The dynamics of the oxidase system. Biochem. Journ., Vol. 18, 1924.

DIXON, M. Studies on xanthine oxidase. V. The function of catalase. Biochem. Journ., Vol. 19, 1925.

DIXON, M., and SYLVA THURLOW. Studies on xanthine oxidase. VI. A cell oxidation system independent of iron. Biochem. Journ., Vol. 19, 1925.

THURLOW, SYLVA. Studies on xanthine oxidase. IV. Relation of xanthine oxidase and similar oxidising systems to Bach's oxygenase. Biochem. Journ., Vol. 19, 1925.

DIXON, M. Studies on xanthine oxidase. VII. The specificity of the system. Biochem. Journ., Vol. 20, 1926.

DIXON, MALCOLM, and KEIZO KODAMA. On the further purification of the xanthine oxidase. Biochem. Journ., Vol. 20, 1926.

KODAMA, KEIZO. Studies on xanthine oxidase. VIII. The oxidation-reduction potential of the oxidase system. Biochem. Journ., Vol. 20, 1926.

MORGAN, EDWARD JAMES. The distribution of xanthine oxidase. I. Biochem. Journ., Vol. 20, 1926.

COOMBS, H. I. Studies on xanthine oxidase. IX. The specificity of the system. II. Biochem. Journ., Vol. 21, 1927.

BERNHEIM, F., and M. DIXON. Studies on xanthine oxidase. X. The action of light. Biochem. Journ., Vol. 22, 1928.

DIXON, M., and H. E. TUNNICLIFFE. The oxidation of reduced glutathione and other sulphydryl compounds. Proceedings of Royal Soc. B., Vol. 94, 1923.

FLEISCH, A. Some oxidation processes of normal and cancer tissue. Biochem. Journ., Vol. 18, 1924.

MOYLE, D. M. A quantitative study of succinic acid in muscle 1. Biochem. Journ., Vol. 18, 1924.

NEEDHAM, JOSEPH, and DOROTHY MOYLE NEEDHAM. The oxidation-reduction potential of protoplasm. "Protoplasma," Intern. Zeitschr. f. physikal. Chemie d. Protoplasten, Bd. 1, 1926.

ONSLOW, MURIEL WHELDALE, and MURIEL ELAINE ROBINSON. Oxidising enzymes. IX. On the mechanism of plant oxidases. Biochem. Journ., Vol. 20, 1926.

DIXON, M. On the mechanism of oxidation-reduction potential. Proceedings of Royal Soc., B., Vol. 101, 1927.

BERNHEIM, FREDERICK. The specificity of the dehydrases. The separation of the citric acid dehydrase from liver and of the lactic acid dehydrase from yeast. Biochem. J., Vol. 22, 1928.

QUASTEL, JUDA HIRSCH, and MARGARET DAMPIER WHETHAM. The equilibria existing between succinic, fumaric, and malic acids in the presence of resting bacteria. Biochem. Journ., Vol. 18, 1924.

———. Dehydrogenations produced by resting bacteria. Biochem. Journ., Vol. 19, 1925.

QUASTEL, JUDA HIRSCH. Dehydrogenations produced by resting bacteria. IV. A theory of the mechanism of oxidations and reductions in vivo. Biochem. Journ., Vol. 20, 1926.

QUASTEL, J. H., and BARNET WOOLF. The equilibrium between l-aspartic acid, fumaric acid and ammonia in presence of resting bacteria. Biochem. Journ., Vol. 20, 1926.

QUASTEL, JUDA HIRSCH, and WALTER REGINALD WOOLDRIDGE. Experiments on bacteria in relation to the mechanism of enzyme action. Biochem. Journ., Vol. 21, 1927.

———. The effects of chemical and physical changes in environment on resting bacteria. Biochem. J., Vol. 21, 1927.

QUASTEL, J. H. The study of "resting" or non-proliferating bacteria. The Journal of Hygiene, Vol. 28, 1928.

———. Quelques travaux récents sur les actions chimiques des bactéries. Leur relation avec les problémes de fermentation. Communication présentée au Congrès International de la Vigne et du Pin Maritime. Bordeaux, 1928.

QUASTEL, JUDA HIRSCH, and WALTER REG. WOOLDRIDGE. Some properties of the dehydrogenating enzymes of bacteria. Biochem. Journ., Vol. 22, 1928.

STEPHENSON, MARJORY. On lactic dehydrogenase. A cell-free enzyme preparation obtained from bacteria. Biochem. Journ., Vol. 22, 1928.

4. A. HAHN AND COLLABORATORS

HAHN, AMANDUS, and W. HAARMANN. Über die Dehydrierung der Bernsteinsäure. Zeitschr. f. Biol., Bd. 86, 1927.

———. Über die Dehydrierung der Bernsteinsäure. Zeitschr. f. Biol., Bd. 87, 1928.

———. Über die Dehydrierung der Aepfelsäure. Zeitschr. f. Biol., Bd. 87, 1928.

———. Über die Dehydrierung der Aepfelsäure. Zeitschr. f. Biol., Bd. 88, 1929.

HAHN, AMANDUS, E. FISCHBACH, and W. HAARMANN. Über die Dehydrierung der Milchsäure. Zeitschr. f. Biol., Bd. 88, 1929.

5. HANS V. EULER AND COLLABORATORS

EULER, HANS V., and RAGNAR NILSSON. Zur Kenntnis der Reduktase (Dehydrogenase) der Hefen. I. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 149, 1925.

———. Zur Kenntnis der Oxydo-Reduktase (Dehydrogenase) der Hefen. II. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 151, 1926.

———. Zur Kenntnis der Reduktase (Dehydrogenase) der Hefen. III. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 152, 1926.

———. Zur Kenntnis der Reduktase (Dehydrogenase) der Hefe. IV. Versuche zur Isolierung der Co-Reduktase. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 155, 1926.

———. Zur Kenntnis der Reduktase (Dehydrogenase) der Hefe. V. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 162, 1926.

———. Über die spezifischen Aktivatoren der Gärungsenzyme. I. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 162, 1926.

EULER, HANS V., RAGNAR NILSSON, and BRITA JANSSON. Co-Zymase X. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 163, 1926.

EULER, HANS V., KARL MYRBÄCK, and RAGNAR NILSSON. Gärung, Phosphorylierung und Oxydo-Reduktion und ihr Co-Enzym. Sv. kem. tidskr., Bd. 11, Jg. 38, 1926.

NILSSON, RAGNAR, and THOR LÖVGREN. Beiträge zur Kenntnis der Phosphorylierung und Oxydo-Reduktion. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 164, 1927.

EULER, HANS V., RAGNAR NILSSON, and BRITA JANSSON. Glykogenabbau im Muskel. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 165, 1927.

EULER, HANS V., RAGNAR NILSSON, and DAGMAR RUNEHJELM. Zur Kenntnis der Hexosen-Redoxase der Leber. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 167, 1927.

———. Über die biologischen Abbau- und Veratmungsvorgänge an verschiedenen Stoffgruppen. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 169, 1927.

NILSSON, RAGNAR, and BRITA JANSSON. Vergleichende Messungen über Oxydo-Reduktion und CO_2-Entwicklung durch Hefen-Enzyme. A. Das Verhältnis von Redoxase-Aktivität und Zymase-Aktivität in Hefe. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 169, 1927.

EULER, HANS V., and KARL MYRBÄCK. Zur Kenntnis der Co-Zymase und des enzymatischen Kohlenhydratumsatzes. Ark. f. Kemi, Mineralogi o. Geologi, Bd. 9, 1927.

EULER, HANS V. Affinitätsprobleme. IV. Ark. f. Kemi, Mineralogi o. Geologi, Bd. 9, 1927.

EULER, HANS V., and KARL MYRBÄCK. Zur Kenntnis des Hexose spaltenden Enzym-Systems im Muskel. Sv. kem. tidskr., Bd. 39, 1927.

EULER, HANS V., and EDV. BRUNIUS. Zur Kenntnis der Mutase. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 175, 1928.

MYRBÄCK, KARL, HANS V. EULER, and ERIK SANDBERG. Über die Aldehydmutation von Essigbakterien. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 175, 1928.

EULER, HANS VON, and RAGNAR NILSSON. Affinitätsprobleme. 5. Ark. f. Kemi, Mineralogi o. Geologi, Bd. 10, 1928.

6. DIFFERENT AUTHORS

ADAMS, R. DOROTHY. Investigation on the crystalline lens. Proceed. Roy. Soc. Ser. B., Vol. 98, 1925.

ACKERMANN, D., K. POLLER, and W. LINNEWEH. Über das Verhalten des Trimethylaminoxyds im intermediären Stoffwechsel als biologischer Wasserstoffacceptor, besonders Sulfhydrylgruppen gegenüber. Zeitschr. f. Biol., Bd. 85, 1927.

BATTELLI, F., and STERN, LINA. Nature des ferments oxydants et des ferments réducteurs. Comptes rendus Soc. Biol., Vol. 83, 1920.

———. Le mécanisme d'action des ferments oxydants et des ferments réducteurs. Arch. internat. de Physiol., Vol. 18, 1921.

BACH, A., and D. MICHLIN. Über die sog. Succino-Dehydrase. Ber. d. Dtsch. Chem. Ges., Jg. 60, 1927.

BACH, A., and K. NIKOLAJEV. Sind sauerstoffübertragende Enzyme mit wasserstoffübertragenden identisch? Zürnal eksperimentalnoij biologii i mediciny, Jg. 1925, Nr. 2.

BERGMANN, MAX, and FERDINAND STERN. Über Dehydrierung von Aminosäuren. Liebigs Annalen, Bd. 448, 1926.

BERGMANN, MAX, ERICH KANN, and ARTHUR MIEKELEY. Über Dehydrierung des Asparagins und seine Verwandlung in Brenztraubensäure. Liebigs Annalen, Bd. 449, 1926.

BERGMANN, MAX, and ARTHUR MIEKELY. Neue desmotrope Aminosäureanhydride vom Piperazintypus. Zur Kenntnis des Abbaues der Aminosäuren. Serin als Dehydrierungsmittel. Liebigs Annalen, Bd. 458, 1927.

BERGMANN, MAX, and HELLMUT ENSSLIN. Dehydrierung gesättigter Aminosäuren durch ungesät-

tigte Aminosäuren. Hoppe-Seyler's Zeitschr. f. Physiol. Chem., Bd. 174, 1928.

Cascio, G. Lo. Sui fermenti dei tessuti e dei liquidi oculari. Annali di ottalmol. e. clin. oculist., 50, 1922.

Dakin, H. D. The action of muscle tissue on fumaric, maleic glutaconic and malic acids. Journ. of Biolog. Chem., Bd. 52, 1922.

Einbeck, H. Über das Vorkommen von Bernsteinsäure im Fleischextrakt und im frischen Fleische. Zeitschr. f. physiol. Chem., Vol. 87, 1913.

———. Über das Vorkommen der Fumarsäure im frischen Fleische. Zeitschr. f. physiol. Chem., Vol. 90, 1914.

Fischer, F. Gottwalt. Zur Kenntnis der Succino-Dehydrase. Ber. d. dtsch. chem. Ges., Jg. 60, 1927.

Harada, Yataka. Studien über intermediären Kohlenhydratumsatz. Über Muskeldehydrasen. Biochem. Zeitschr., Bd. 164, 1925.

Keilin, D. On cytochrome, a respiratory pigment, common to animals, yeast, and higher plants. Proceed. Royal Soc. B, Vol. 98, 1925.

———. A comparative study of turacin and haematin and its bearing on cytochrome. Proceed. Royal Soc. B, Vol. 100, 1926.

———. Cytochrome and respiratory enzymes. Proceed. Royal Soc. B, Vol. 104, 1929.

Kirchner, O. Bioskopische Reduktionsmethoden I. Der Wert der Nitroreduktionsmethode als absolut-quantitative Methode. Arch. f. Hygiene, Bd. 95, 1925.

———. Bioskopische Reduktionsmethoden II. Vergleichende Untersuchungen mit der Nitro- und Methylenblaureduktionsmethode und ihre Verwendbarkeit für Stoffwechseluntersuchungen an Bakterien. Arch. f. Hygiene, Bd. 96, 1925.

Knoop, F. Über die Stickstoffbindung bei der Eiweisssynthese in der Natur und das Interesse der Biologie an den physiologischen Oxydationsreaktionen und ihrer Umkehrbarkeit. Münchener Mediz. Wochenschr., Nr. 51, 1926.

Lebedew, A. Über das vermeintliche Co-Enzym der Oxydoredukase. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 172, 1927.

———. Über die Wirkung der Oxydoredukase der Hefe auf einige vermutliche Zwischenprodukte der alkoholischen Gärung und auf Crotonaldehyd. Hoppe-Seyler's Zeitschr. f. physiol. Chem., Bd. 172, 1927.

Lipschitz, Werner. Colorimetrische Messung der Zelloxydationen durch Reduktion von Nitrokörpern und Nitraten. Die Methodik der Fermente von C. Oppenheimer u. L. Pincussen, 1928.

Lundquist, Carl Wilhelm and Gösta Rylander. Om bakteriers förmåga att reducera methylenblått samt en förbättrad metodik för studiet av densamma Hygiea, 1927 (Stockholm).

Löffler, Ernst, and Rudolf Rigler. Über die Atmung der Bakterien durch Methylenblaureduktion. Versuche an der Typhus-Coli-Gruppe. Zentralbl. f. Bakteriol. Parasitenk. u. Infektionskrankh., Bd. 99, 1926.

Meyerhof, Otto. Über die Atmung der Froschmuskulatur. Pflüger's Arch., Bd. 175, 1919.

Stern, Lina. Über den Mechanismus der Oxydationsvorgänge im Tierorganismus. Jena, 1914.

———. Die Beziehung des Katalasesystems zu den Oxydationsvorgängen in den Tiergeweben. Biochem. Zeitschr., Bd. 182, 1927.

———. A propos du mécanisme d'action des catalyseurs oxydants. Cpt. rend. des séances de la Soc. de Biol., Vol. 98, 1928.

Szent-Györgyi, A. v. Über den Mechanismus der Succin- und Paraphenylendiaminoxydation. Ein Beitrag zur Theorie der Zellatmung. Biochem. Zeitschr., Bd. 150, 1924.

———. Studien über die biologische Oxydation. II. Über den Mechanismus und die Bedeutung der SH-Katalyse. Biochem. Zeitschr., Bd. 146, 1924.

———. Studien über die biologische Oxydation. III. Über das Oxyd der SH-Gruppe und über die Oxydation durch Äthylperoxyd. Biochem. Zeitschr., Bd. 149, 1924.

———. Zellatmung. IV. Über den Oxydationsmechanismus der Kartoffeln. Biochem. Zeitschr., Bd. 162, 1925.

———. Über die Wirkungsweise des Schardingerschen Ferments. Biochem. Zeitschr., Bd. 173, 1926.

Tsubura, Shiro. Studies on the physiology of plain muscle. III. Comparison of the reducing properties of plain and striated muscle. Biochem. Journ., Vol. 19, 1925.

Warburg, Otto. Über die katalytischen Wirkungen der lebendigen Substanz. (Arbeiten aus dem Kaiser Wilhelm-Institut für Biologie. Berlin.) Berlin, 1928. (Collected papers of O. Warburg on these subjects.)

BIOLOGICAL PROBLEMS AND OPINIONS

By EDWARD J. v. K. MENGE

Marquette University

HAVING just celebrated the centenary of the first successful attempt at manufacturing an organic product in the laboratory, it is fitting that the eye of scientific men should scan the century, take pride in the marvelous progress of the biological sciences, search for the causes of failure and evaluate experimental evidence and philosophical interpretations. It is further fitting that we should know what the contributions of men of all lands have been, lest we fall into the common error of non-scientific men—that of assuming that because a problem, a fellow worker, an emphasis, or a philosophy of life is close at hand, and thus considered important by friends and coworkers, it therefore takes precedence over all the remaining universe.

The history of science during the nineteenth century has been written so well by those who have preceded us that it would be presumptuous on my part to try to improve upon it. Not so much, however, has been written regarding our own generation, or the work of men still with us. Consequently, this paper is to be confined to a statement of what the ablest present-day workers in the biological sciences believe to be important and well worth while.

Yet here again the field has become so vast, the work so varied, and the contributions so numerous that one may well throw up one's hands in dismay, especially when it is noted that the editors of *Biological Abstracts* have listed forty-seven major subjects under which to classify the work of biologists. And each of these forty-seven major subjects has at least one or more subheadings or branches of biology in which men are specializing.

If Johannes Müller, as it is often stated, broke down mentally trying to keep abreast of the literature on physiology about the year 1857, when physiology had but just come into existence during his lifetime, how can any one person even approach success in such a plan now, when thousands upon thousands of papers are being published annually?

I do not believe that anyone can do so successfully, nor does this paper make any claims towards furnishing even an approximately complete answer. I have, therefore, asked the heads of departments of biology and zoology in all the universities of the world, outside the United States, and also twenty of our own most distinguished biologists, to give me their mature thought on the matter. This paper, then, represents, not the opinion of any one man, but the consensus of opinion of the world's most important biologists and zoologists.

These same distinguished scientists, leaders in their respective branches of biology from every country of the world, here then speak for themselves. I shall not evaluate, but attempt to state the case and so produce a living document at least of interest to the younger workers in the field.

Seventeen years ago, C. S. Minot of Harvard, then Exchange Professor at the

Universities of Berlin and Jena, delivered six lectures on *Modern Problems of Biology* at the latter institution. The six problems discussed were:

1. The New Cell Doctrine
2. Cytomorphosis
3. The Doctrine of Immortality
4. The Development of Death
5. The Determination of Sex
6. The Notion of Life

A Survey of National Trends in Biology, dealing with the problems of biology as they appear to the biologists of all nations seventeen years later, should prove interesting.

It is undoubtedly true that science should know no political boundaries, and that as biology is a science, it should be international. However, one need be in correspondence with but a very few biologists to find that while biology may be international, biologists certainly are not.

In the answers received from the various biologists and zoologists to my query there is reflected the same national feeling that one would find in men whose training, or lack of it, is not expected to help them control their emotions or to render impartial judgment on matters that come before them.

As the answers continued coming in, a great temptation presented itself to call this paper *The Psychological Reactions of Biologists*, but a calmer judgment prevailed.

Political, religious, educational and traditional boundaries are so much a part and parcel of the human individual that, try as he will, he can never avoid being influenced by them.

Here comes one letter filled with the bitterness of life by virtue of his country's partition, leaving but "an insignificant group of hillocks," as he puts it, which men now force him to call by the name of a country for centuries great and glorious. He no longer feels he has a Fatherland. For him, his country has ceased to exist. There comes another breathing of hope and looking with patriotic enthusiasm to a wondrous future following the birth of a new Fatherland whose racial and national ambitions have had to lie dormant since time immemorial.

Let us first note in what specific fields of biological endeavor the majority of experimenters have been working during our generation, and what it was that gave the impetus to such work.

GEOGRAPHY AND BIOLOGICAL INTERESTS

While all nations have many men employed in various departments there are nevertheless certain more or less specific fields in which the majority of the workers of any specific country find themselves primarily interested, this being due to geographical conditions rather than to political boundaries. For instance, one finds Canada and the Scandinavian lands with vast coast lines always interested in fisheries and all that relates to them. But we shall let the Norwegian biologist, Hjalmar Broch, speak for himself:

> A survey of the biological work in Norway in many respects shows that geographical conditions play a predominant part. On the one hand we are situated in the periphery, and we see how "modes" prevail in theoretical studies. During the first years of the century the cytological mania, which had already culminated in Central Europe, also made its way to our university, and gradually faded away again some time after it had played out its predominant part in Germany. Then studies of heredity made their way northward, and are at present *à la mode* to a degree that every student of biology finds it his duty to bestow a tinge of this on his theme however far the latter in reality may be apart from the field of heredity investigations. In many cases we can trace this mania backward to the rise of certain leaders of little originality who wish to be *à la mode*, so as to get a place among the real leaders of the epoch.
>
> There is, however, one field of biology that runs like a real thread through the history of Norwegian

biological science—the ocean. From the earliest times our nation has been a nation of sailors and fishermen, and it was from the beginning but natural that the attention of Norwegian biologists should also be roused by the sea, the country having a coastal line of more than 3000 kilometers, whereas its breadth is in most parts quite small.

The great traditions given by such zoologists as Johan Ernst Gunnerus, Michael Sars, and Georg Ossian Sars, have naturally put their stamp on Norwegian biology, and therefore the most important biological contributions are naturally connected with marine research.

Likewise in Canada, considering biology as it applies to economics and industry, we find that the most important effort mentioned is that of the coöperative development by the Canadian universities of economic fisheries research, including the formation of the Biological Board of Canada, and the establishment of marine laboratories. There is Saunders' work on Marquis wheat, which has made "millions for Canada," and better still, it has created the atmosphere of economic adjustment of plants and animals to northern environments. The production of Marquis wheat, a pure example of the older selective breeding, was the direct response of a practical minded man to solve a particular Canadian or northern American problem of high yield and short season.

In the United States and in other countries, where many new types of plants have been imported, an international exchange of both useful and deleterious insects has been made. Entomological work of ascertaining "which is which" and trying to bring back that much needed balance in nature which keeps plants in good health and growth, also has been pursued. Many insect pests flourish in their new homes because those particularly predaceous and parasitic insect enemies which ordinarily keep them in check are not imported with them. But an interesting work has grown up in finding what these insect enemies are and importing them.

In connection with work of this nature, one can show how some of the larger animals may be, and are, conserved by international coöperation. Vernon Kellogg calls attention to the fur seals of the Pacific, which were rapidly approaching extinction on account of unrestricted killing on the high seas as well as on their breeding grounds in the Pribilof Islands, when international agreements made in 1911 among Great Britain, Russia, Japan, and the United States saved them as a species and at the same time allowed a reasonable taking of skins.

This geographical aspect is also prominent in the report of the 1926 meeting of French scientists. Owing to economic conditions the Colonies must be developed. President Alfred Lacroix particularly stressed the part that science must play in the development of Tunis, Algeria, Morocco, Senegal-Niger, Guinea, the Congo, Indo-China, and other regions under French control. In fact, that year's meeting of the French association was held in Constantin, Algeria. Even Dr. Voronoff, the gland surgeon, has passed from human gland transplantations to work on farm animals, with a view toward producing heavier sheep bearing more wool. And Australia, a very few years back, spent something like $600 per man to bring a group of scientists to its shores, hoping that some of her own particular problems would and could thus be solved.

Nearly all biologists consulted thought that the economic side of their science was of considerable, though by no means of greatest importance, and by this term some included everything in the way of human relationships. In fact, the term "human biology" is used by several, referring to the relations of man to his environment, that is, to the way biology is applied to

economics, to medicine, to education, to sociology, and to psychology.

In the United States biological workers have been employed probably chiefly in experimental general biology, in genetics, in embryology, in cytology, in tissue culture, and in general physiology.

In genetics the impetus came through the work of Mendel, Weismann and Roux in European countries, and in the United States through that of Wilson and Morgan.

J. Stanley Gardiner, of Cambridge, holds that history fertilizes the scientific soil, and that there is a considerable correlation of science with any profound disturbances which cover wide areas. Thus

> China for 6000 years has altered very little and shows little advance. Our great advances in Europe are correlated with (1) the dominance of Spain and the profound wars in the 16th century; (2) the Cromwellian and other troubles in Europe of the 17th and early 18th centuries; (3) the Napoleonic times was a great advance; (4) 1850 with its revolutions or attempted revolutions, and (5) the last 20 years has been a time of great unsettlement and difficulty; where we are going now, I do not know; I expect we are in the stodgy period, but in 40 or 50 years we may have a world cataclysm which will stimulate people afresh.

A general survey of the literature on biology of the past thirty years demonstrates that the earliest investigators by no means always had enough facts at hand on which to build their speculations, but one may add that such lack of facts by no means lessened the output of speculation. However, an amount of good work was done, so that one really did obtain more exact anatomical and physiological data, especially in cytology and neurology. Much of the advance in the latter subject was due to the excellent work of the Spaniard, Ramon y Cajal. Considerable promotion and dissemination of biological knowledge through various periodicals then took place, which in turn stimulated general interest enough so that provision was made for specially equipped laboratories.

But merely extending knowledge a step further is not developing science. Breeding homing pigeons that could cover a given space with ever increasing rapidity did not give us the laws of telegraphy, nor did breeding faster horses bring us the steam locomotive. The so-called improvements of the microscope pertain to improving the stands rather than the lenses. Until a new principle of optics is discovered the microscope remains what it is.

One can say of other fields of work what the late E. W. Scripps said of the ocean, "Why, of course, everything anybody can learn by investigating the ocean and the organisms that live in it will be useful to somebody in some way, sometime." But the real advance in science does not come from merely extending what we have, but very often from uncovering a slightly hidden something that we are permitted to use, and to work out some general law or principle from this. The problem is not, as Morgan says, "to discover how many kinds of structures exist, but whether there are common principles that run through them all. If there are no such principles, then we are indeed headed toward chaos."

Applying this thought to his particular work, he continues:

> Although we have not gone very far in our analysis there is encouragement to go on. If one takes the cell-division in all its diversity, we shall not get very far by studying all the many variations resulting from slight differences in the structure of eggs of every species, but we shall really have succeeded in accomplishing something worth while if we find a few simple physical *principles* involved in that cell-division.

And so, too, one must not place credit for any given finding in the wrong place. Several writers of note have pointed out

that chattel slavery was quite necessary in one state of civilization if men were to make any progress and have any assurance of even an immediate success in their varied efforts. Then, too, it was not abolished because humanitarianism abhorred it, but because another type of civilization was brought about by the invention of the steam engine, which made it possible to sustain civilization without slavery. So, too, modern democracy did not evolve from any interest in the brotherhood of man, but because discovery and exploration opened up entirely new channels into which men's lives could flow and lead an independent and self reliant existence.

Now let us examine the biological literature and the letters received to see what the biological world considers important. One is struck immediately by the practical agreement of the biologists of all nations as to what is important and what has been done, during the past quarter of a century, that is of lasting value.

MENDELISM

One finds that after almost a half century of experimentation with just one idea in mind—of finding new angles by which to demonstrate evolution—a sigh of relief went up that other fields had finally been opened. Yet paradoxical as it may seem, the finding of the very factors which opened new fields had its rise in the discovery, or rather rediscovery, of a piece of work which in turn was the cause of producing another theory of evolution, namely, De Vries' theory of mutation. The rediscovery and verification came about, simultaneously, by De Vries in Holland, Correns in Germany, and Tschermak in Austria. These men gave to this generation a knowledge of an outstanding piece of work—a work consisting of many experiments carefully performed and carried on throughout a great length of time by Johann Gregor Mendel. Mendel's work was actually done in a preceding generation, but as it remained unknown until our own, and as it has exercised the profoundest influence on all biological work since 1900, it deserves a place in this survey.

Mendel pointed out that definite numerical results were to be obtained in crossing peas, which he explained by two simple hypotheses—that of segregation and that of independent assortment.

The first of these is now accepted as a 'law' having a very wide application. All later discoveries in the field of heredity and genetics rest upon that law. It is, as Morgan says, "a broad generalization based on numerical data and allows us to predict with accuracy the outcome of a given solution."

Practically all these biologists whose opinion was asked were unanimous in putting the experimental work on genetics and heredity in the foremost rank of this generation's achievement.

Mendel's second hypothesis applied only within certain limits that can be accurately stated, but both hypotheses hold very definitely for the cases he studied and for characters of the majority of plants and animals studied since then. However, much knowledge has been added, in the way of additional facts, so that we now speak of a 'linking' and a 'crossing-over' of certain characters and with such equipment added, we apply the laws over a much wider field than Mendel did or could.

Much of the difficulty of early workers in any new field is that they are unable to formulate a question so as to get an intelligent answer, and much of the objection and faultfinding regarding Mendelism is probably due to this same fact.

ENTWICKLUNGSMECHANIK

Any new idea thrown into the biological arena would not only cause great numbers of men to follow experimentally the lead thus given, but the lesser leaders would be inclined to break into new paths also, though usually into closely related fields. So we find papers on genetics and heredity with emphasis on variation appearing one after another, and almost simultaneously, others on behavior and physiology. This work on physiology concerned itself primarily with the reactions of mature organs, and did excellent work for "medicine." A little later others drove the problem further back and the question of how the organism arose in the first place was given a niche in the gallery of experimentation. However, this beginning of embryology was largely descriptive, accounts being written merely of what was seen. From this descriptive work, in turn, real experimental embryology was born. Now men such as William Roux and Hans Driesch began destroying or removing parts of the early embryo to ascertain what would happen.

Roux's single pioneer experiment of note consisted in killing one of the first two cells of the dividing egg of a frog. The remaining half produced only a half embryo. Driesch, on the other hand, found that with one half egg of a sea urchin destroyed, the remaining half developed into an entire organism. Driesch finally showed that the apparent difficulty lay in the physics of the various eggs used for the experiment. In some cases the usual method of egg division caused one portion to be heavier than another and thus to sink into the surrounding nourishment. When the heavier part was removed, the lighter portion received but little or no nourishment, and consequently could not develop. If, however, one used an egg such as that of the sea urchin or even of the frog and placed it so that nourishment was forthcoming, then each portion of the egg would result in a completely formed, but often somewhat smaller, animal.

Driesch finally came to the conclusion that to him at least, there was always something over and above what the laboratory could find in the development of a complete organism from such separate parts. He and his followers therefore took the stand that satisfactory explanations are more likely to come from an investigation of the essence of life than from any purely embryological and physiological experimentation in the laboratory.

PHYSIOLOGY

Here was a parting of the ways. Many sought to retrace their steps and to start anew. Thus some became interested in behavior, and from behavior of the entire higher organisms, or parts of those organisms, there was the inevitable tendency to go farther and farther back. If all life was but the working out of actions and reactions of masses of cells, and cells in turn were composed of protoplasm, it was but logical that one should study protoplasm. This was not only a fruitful field for an analysis both physically and chemically of the substance of protoplasm itself, but of the behavior of the single celled plants and animals, which being actual living organisms, must have within their single cell the answer to the riddle of life.

Physics had won first place in the sciences for four reasons: (1) it accepted the uniformity of nature, (2) it insisted upon exact measurements, (3) it concentrated attention on the regularities that underlie the complexities of phenomena as they appear to us, and (4) it emphasized the importance of crucial experiments.

It was but natural that physiology should try to do with organs what physics

did with inanimate material. Thus the study of mere reactions came into being, so that first we wanted to find out the actual chemical make-up of the material with which we were working and then how it would react to all manner of stimuli as a whole, as when, for instance, certain portions were eliminated. From the grosser experiments there was a resort to finer ones, and here a single organism was taken and subjected to all manner of "indignities" to see how this particular thing would react under very particular and definite excitations. But again, biological workers landed in the same type of *cul-de-sac* in which Driesch had landed.

As J. Arthur Thomson says

> the chemical-physical formulations do not actually describe what we see and know. If complete they would afford a ledger of all the chemical and physical transactions that go on in the body, but that would not describe the organism's apparently unique qualities as in integrated living individuality, such as the power of enregistering its experiences within itself so that subsequent behavior is influenced. As science is at present it is necessary to use special biological categories describing the life of the organism—notably its growing, reproducing, developing, varying, endeavoring. For isolated transactions in corners of the body, the chemical-physical description may suffice, but not at present for anything like behavior.

THE GENE

Let us retrace our steps for the moment to the birthday of a single little fruit fly in 1910, which happened to be born with white eyes. We find this seemingly insignificant animal the chief factor in furnishing an impetus toward a study of heredity and genetics, which has brought forth what many biologists consider the nearest approach to the solution of any biological problem yet presented.

The impetus this solitary fruit fly gave to the study of heredity and genetics has brought us to the belief that each chromosome is made up, in turn, of a chain of separate particles which we call "genes," because it seems that they are the very basis on which the genealogy of the individual rests.

Maybe each chromosome has thousands of these genes, and probably no two are alike. The individual plant or animal is the product of the activity of all the genes together, while heredity is the result of the shuffling of these genes in each generation.

Quoting T. H. Morgan, who is the outstanding American in this field of work:

> In several plants and animals we can refer these genes to particular chromosomes, and in one animal at least, about four hundred genes have been placed. On the assumption of their relative positions with respect to one another, we can predict what the numerical results will be in inheritance for some four hundred different characters. The theory justifies itself in that it allows one to predict the outcome in terms of numbers for all these four hundred characters whose genes have been located.
>
> The genes divide when the chromosomes divide, and collectively their division is what we see when each chromosomal rod splits throughout its length. It is the genes that come together with extraordinary precision, which implies probably that we are dealing with events of a molecular order. We can go no further until physics has furnished us with a key to unlock these extraordinary events.

Boveri's work on the mechanics of cytology must not be left unmentioned at this point.

So far we have discussed the work on cytology, genetics, and heredity, embryology and regeneration, and physiology with its subheadings of physics and chemistry. One should not forget the exceptionally interesting and valuable work on tissue cultures outside the body of the individual in which they originally grew, done by Ross G. Harrison and Alexis Carrel. These men were able to take individual cells and groups of cells and keep them alive and in apparently good health quite outside of their usual habitat.

The work on the possibility of artificial

parthenogenesis by Yves Delage and Jacques Loeb also belongs in this field. A mere pricking of the frog's egg with the point of a glass or platinum needle and then washing the eggs in blood, will produce fatherless frogs. In other cases a chemical or physical change of the water in which the eggs are placed will cause unfertile eggs to develop.

Baltzer's work with the green worm of the Mediterranean and the North Seas seems to show that sex may be determined by either environment or food, or a combination of both, for he was able to produce intermediate sexes by merely shaking, from their usual position, those which would ordinarily have become males, and forcing them to grow in a foreign medium.

The work of H. S. Jennings on the behavior of the lower organisms seems to demonstrate some "purposive behavior" even in animals of a very low level. Such experimental work as having a brainless starfish attack and conquer an equally brainless, but none the less formidable, sea urchin may throw much light on some future experimental psychology.

Closely akin to this type of experimentation is that of the various "tropisms"—the name given to those "ingrained constitutional obligations to adjust the body so that the two sides, perhaps the two eyes, ears, or nostrils, are equally stimulated" to secure a physiological equilibrium.

Thus the young eel or elver goes straight upstream, the male mosquito finds the buzzing female, and the moth flies into the unnatural stimulus of the candle. Somewhat higher is the persistent way in which newly hatched loggerhead turtles make for the open horizon, as Professor G. H. Parker has shown, which usually and happily means finding the sea.

Finally, one may add the work done in comparative psychology, and the attempt to show what effect the "mental" has had in determining the path of evolution.

In this connection also, should be mentioned the work of Robert Chambers in developing a technique of microscopic dissection, which opens up a field yet unexplored, and that of Professor Pregl of Graz, who has done outstanding work on the ultramicroscope and developed new methods in microanalysis.

From an agricultural point of view, a valuable answer has been found for such questions as, "How can we, even by an importation of many different types of plants and animals, each susceptible to differences in temperature, climate, soil, moisture, and disease, keep that particular balance in nature which modern transportation is continually upsetting, by importing with such plants and animals those particular parasites, which will keep or again bring back that particular balance in nature so much needed"—by the workers in applied entomology well represented by such a man as L. O. Howard, who has furnished some of our most stimulating answers.

VITAMINS

In biochemistry, the paper of Hopkins and Willcock *Amino Acids in Metabolism*, in 1907, foreshadowed the very important discovery of vitamins. Here it is shown that there are accessory food factors in the growth of an organism which cannot be chemically analyzed.

Indirectly correlated with this field in its scientific aspects is the work of Dr. Allen on the *Artificial Culture of Marine Plankton Organisms*. His study showed that organisms, when developed artificially, require that chemically pure solutions be sensitized by natural waters before they can live and breed in them.

The work on vitamins, the discovery of their production in relation with sunlight, etc., is of great concern not only to the health of man, but of considerable prac-

tical utility in connection with the production of his food supplies.

Under biochemistry one should certainly mention what J. Arthur Thomson considers one of the great milestones in biology—the discovery of a "glutathione" by Sir F. Gowland Hopkins in 1921. This is an organic substance widely distributed in plant and animal cells, which acts as an "oxygen transporter," that is, as an intermediary between the oxygen of the air and the food-materials of the tissues. Its biological importance is due to the fact that "this transporter and liberator of oxygen accounts for the energy-yielding combustions that take place at a low temperature within the living cell. It explains how the cell burns and yet is not consumed."

D. Keilin's discovery of the cell-pigment "cytochrome," which has something to do with the control of oxygen within the cell, should also be mentioned.

Finally, Professor Baly's discovery of artificial photosynthesis should not be forgotten. Baly's work made possible the forming of organic compounds such as formaldehyde from water and carbon dioxide, which process, in turn, formed sugar.

Nearly all biologists placed the work on endocrines as among the most notable achievements of this generation. Thomson says of these so-powerful factors in the lives of all organisms that they are chemical messengers which are like "keys that open certain doors and close others, and they exert a regulative action on many of the functions of the body, securing their orchestration or correlation."

The discovery of this chemical integration has changed the whole face of physiology. Biologically regarded, the hormones, such as adrenalin and thyroxin, enable the biologist to understand not only everyday events such as the cat's hair standing on end before the intruding dog, but the changes that come in adolescence when hormones from the reproductive organs saturate throughout the body, and activate the growth of the stag's antlers, the swelling of the frog's first finger, and scores of other adolescent novelties.

MEDICAL BIOLOGY

The most spectacular work in preventive medicine, which really belongs in this century because real effective proof of its working out was not forthcoming until 1900 or thereafter, is that of the discovery of how malaria and yellow fever are carried, followed by the exceptionally effective methods used in applying this knowledge in those regions where the disease was ever a source of dread and death. It was a Latin American, Carlos Finlay, who was really the pioneer in yellow fever work and a Brazilian, Oswaldo Cruz, who saved the lives of untold millions by his intelligent application of the principles that Finlay and Reed discovered.

One might add the discovery of diphtheritic antitoxin to the list of outstanding medical discoveries that were ushered in at the moment when the nineteenth century was giving way to the twentieth. No longer ago than 1893, where records were kept, some 58 out of every 100 diphtheria cases ended in death. After 1895, with the discovery of antitoxin, there were less than four deaths in every hundred diphtheria cases, provided, of course, that the antitoxin was injected shortly after the onset of the disease.

With typhoid fever, the change in fatalities is even more startling. During the Boer War (1899-1900) with only approximately 208,000 soldiers engaged, there were 57,683 cases of typhoid with 8,022 deaths, while only 7,781 men were actually killed in battle.

Only sixteen years later among the British on the great Western Front during

the World War, with approximately 1,300,000 men, there were in all only 7,500 typhoid cases of which 266 resulted in death. This typhoid comparison is of especial interest because the French did not use the methods employed by the English during the first sixteen months of the war, with the result that their reports show 96,000 cases of the disease with 12,000 fatalities.

One should mention here, also, the discovery of insulin by Banting, which is of far reaching medical import. The story of this piece of research, which ultimately culminated in the discovery of insulin, according to a correspondent had

> a long background of trials as between the known facts of sugar reduction in the body, the immediate necessities of diabetic patients, the existence of corrective substances in the pancreatic secretion and above all the clinical failure of gross pancreatic secretion. It was the idea of utilizing pancreatic material before the normal external secreting cells had developed in the young, coupled with some highly practical knowledge of domesticated animals that gave Banting his opportunity.

F. D'Herelle's discovery of the bacteriophage, the enemy of germs, a "parasite upon a parasite" and not a chemical something, also is considered of great possible importance for the future. Then, too, the extremely important and almost exhaustive researches of Maud Slye upon over 50,000 mice have demonstrated at least one thing in regard to cancer—that both resistance and susceptibility to that dread disease are hereditary in the animals studied.

UNSOLVED PROBLEMS

With this little summary of the outstanding biological work of our own generation, we may pass on to what problems the biologists themselves feel have been actually solved during this period and try to ascertain what they consider the most important problems still unsolved.

All are agreed that no problem has been fully solved, but that, nevertheless, much light has been thrown upon a good many points of interest which will prove valuable for workers of the future, in continuing from where we of this generation have left off.

It may afford the layman an interesting insight into the mind and thought of the biologist to read a letter such as this:

> You ask my opinion as to the most important biological problems of our age! I must confess that I find it utterly difficult to give an exact answer. Any biological problem is of importance, none is superfluous or even of subordinate importance (that is, if you think of biology as a whole and not only as an aid to industry, etc.). Biology is a building that needs every one of its stones—if you take any one of them away the entire building will fall into pieces again. Every biological investigation is of equal importance; i.e., if it is not worked out or followed out into caricature. Only history can in the long run decide and estimate with certainty the sound kernel of each "mode"—every "mode" is bound to be driven in caricature, when its adorers take the last steps into that *cul-de-sac*, where every mania sooner or later comes to an end. Choose whichever instance you will, systematics and classification, phylogeny, cytology, physiology, heredity, etc.—you will, in every case, find that students of biology at last put their heads into the *cul de sac* and cannot get further until they are pulled out by some other partial discipline. The side path was passed by unheeded, because they could not and cannot look in more than a single direction—most biologists have only small horizons. To every age, the problem or problems will seem to be of greatest importance where some of the great personalities of that special epoch casually are leading others.

More than one writer speaks of the "fads and fancies," which have taken hold in biology at various times, and these men call attention to the fact that we have but to examine the scientific journals to see the successive waves of contributions on tropisms, artificial parthenogenesis, cytology, spermatogenesis, regeneration, genetics, tissue culture, endocrines, etc., which have come and gone. There seems to be some one stimulus for such work, which

springs from some particular discovery that promises a way out of the mechanistic dilemma, that is, which promises some light on a mechanistic explanation of living phenomena. Many then start work on a problem and pile up apparently stronger evidence, only to find themselves at sea more than they were before. That particular discovery is then dropped, and work is begun on another, followed by the same result. This procedure necessitates intensive work which leads to quick results, and has its advantages, of course, but instead of following a problem out with some degree of finality, it is given up and another fad is followed.

Back of all experimentation the impetus seems to come from a belief that in the physico-chemical explanation lies the only mode of approach to an understanding of life itself, acceptable to modern man.

Let us then, at this point, try to find what modern biologists consider the most fundamental problems of the day.

Again there is practical unanimity.

(1) The nature of life. That is, does living organic substance differ from the inorganic? While this problem is far from being solved, it seems that the recent work on bacteriophages and the filterable viruses is pushing our horizon to a much lower level.

(2) The discovery of the constitution of protoplasm and its manner of operation.

(3) The problem of the causes of variation, which may in turn be stated as the mechanism of differentiation and the mechanism of evolution.

(4) Cancer research. Cancer is ravaging humanity continually to a greater extent, and practically nothing is known of either its origin, its control, or its cure.

(5) The relation of genetics and environment. Important because so many human problems are affected by genetics, such as disease, sociology, etc.

(6) Disease. Is its predisposition really hereditary, or is it environmental? Is any defect really hereditary or is it induced by environment?

(7) Criminality. Is it hereditary, or is it environmental in its origin? These are decidedly important human problems. Even immigration is affected by the answer.

(8) So-called superior and inferior peoples or races. Are they really such?

(9) Economic entomology. Particularly emphasized because of the growing importance of many species of insects. The interference with the balance of nature converts many insects into potential or actual enemies of man and his products. An enormous amount of work needs to be done in this field.

All agree that the work done on genetics and heredity and in the related fields of physiology and biochemistry has greatly extended man's knowledge of the mechanism of inheritance and the relation of inheritable units to definitive characters resulting in the development of the organism. They also agree that they have thrown considerable light on sex differences and the determination of sex, while the work on the ductless glands has thrown a light on personality and human biology. But these studies also cause us to withdraw our former idea that heredity was everything and environment nothing.

What has really been demonstrated by this work may be summarized as follows:

(1) That heredity is an orderly process, obeying certain very definite laws.

(2) That environment is coequal with heredity. What part each plays is still to be solved, that is, in any given instance *something may be the product of environment or of heredity, but the question of which is the more important can be studied only in the individual case.*

(3) From the philosophical side, that genetics is the single experimental criterion of evolution, and hence of biological philosophy. Its findings have, therefore, forced the withdrawal of science from the welter of speculation into which it had fallen, by establishing experimental tests for the various claims. And finally,

(4) That genetics permits a better valuation of so many problems of disease, of insanity, of feeble mindedness, and of various individual and social problems.

LIST OF LITERATURE

KELLOGG, VERNON L. 1925. On international biology, Bul. Pan American Union, December.

MENGE, EDWARD J. 1930. A Survey of National Trends in Biology, Milwaukee, Bruce Pub. Co. (Contains full bibliography.)

MINOT, C. S. 1913. Modern Problems of Biology. Philadelphia. P. Blakiston's Son & Co.

MORGAN, THOMAS HUNT. 1927. The relation of biology to physics. Science, March 4, pp. 216–219.

RITTER, WM. E. 1924. The Australian meeting of the Pan-Pacific Science Congress. Science, March 28.

THOMSON, J. ARTHUR. 1926. Article 'Biology' in Encyclopedia Britannica, (13th Edition).

SPECIAL SUMMARIES:

1924. Report of the Ninety-Second Meeting of the British Association for the Advancement of Science. President's Address, p. 8.

1926. The French Association for the Advancement of Science, Science. Aug. 13. Under 'Science News.'

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE FUTURE OF THE EARTH.
By Harold Jeffreys.
W. W. Norton and Co., Inc.
$1.00 $4\frac{1}{8}$ x $6\frac{1}{2}$; 79 *New York*

A billion years ago, or so, a wandering star came within the gravitational field of the sun, and through the tidal forces set up, pulled out a long filament of gas. Under the gravitational attraction of its parts, the filament broke up into droplets which later condensed. These are the planets, and one of them is the earth, on which we move and have our being. Another mass was secondarily separated from the earth by the sun and this is our moon. From those early times till now, the temperature on the earth has been fairly constant, with intermittent fluctuations, but in the future things will be colder. The earth obtains almost all its heat from the sun, and the latter as a reservoir is being depleted at an enormous rate; so much so that in another billion years, the ocean will be frozen even at the equator. In the meantime changes will be in process in the relation of the earth and its moon. The tidal forces between these two operated at first to slacken the speed of the earth's rotation and increase the moon's distance. This will continue until the period of rotation of the earth and revolution of the moon are equal to about 45 days. After that the sun will take an upper hand over the moon in its tidal influence on the earth. It will slow the earth still further and the moon will again approach. Then these two will collide.

THE UNIVERSE AROUND US.
By Sir James Jeans. *The Macmillan Co.*
$4.50 $5\frac{3}{4}$ x $8\frac{1}{2}$; x + 341 *New York*

This is one of the more successful of the attempts to present popularly the results of recent advances in physical science. It has been a best seller and deservedly so. Written primarily from the viewpoint of the pure astronomer, it nevertheless does not confine itself to consideration of heavenly bodies. The whole range of physical theory regarding space and matter from the infinitesimally small to the infinitely large is surveyed with beautiful clarity and vividness. In speculative matters the author tends to a pessimistic outlook. Where alternative theories are available,

he prefers the picture of a universe running down constantly and inevitably to a dead level of unavailable energy.

The complaint has been made that in his writings on the origin of the solar system, Jeans has not given sufficient credit to the American contributors to the tidal theory. The charge seems to be substantiated in this volume. Neither Chamberlin nor Moulton is mentioned in the index.

THE STORY OF EVOLUTION. *Facts and Theories on the Development of Life.*
By Benjamin C. Gruenberg.
D. Van Nostrand Co., Inc.
$4.00 6 x 8¾; xvi + 473 *New York*

Dr. Gruenberg has already established a secure reputation as a writer of really sound elementary texts and popular expositions of biology. The present volume will enhance this reputation. It is a sane, well-balanced, entertainingly written, and adequately illustrated popular account of the present state of knowledge about organic evolution and the chief factors which have been concerned in it. It should make an excellent college text, as well as a sound guide to the general reader who wishes to learn, without too great effort, how far along biologists have got with the problem of evolution.

WHEN MAMMOTHS ROAMED THE FROZEN EARTH.
By Heinrich Schutz. Translated from the German by Frank Barnes.
Jonathan Cape and Harrison Smith
$2.50 5½ x 8½; 197 *New York*

A book for young people picturing what the author conceives to have been the trend of events during the closing era of the glacial period. He tells of terrific storms, of fierce animals roaming the earth and battling with one another, of the downfall of the mammoth and the rise of man. Altogether he has a yeasty imagination. The book is more or less thrilling in spots. It perhaps suggests as true an account of what happened in that far off age as it is possible to attain after a lapse of many thousands of years, since it is impossible to check the imagination, except occasionally in regard to a minor detail, in regard to which there are some obvious slips.

JURASSIC FOSSILS FROM JUBALAND, EAST AFRICA, COLLECTED BY V. G. GLENDAY, *and the Jurassic Geology of Somaliland. Monographs of the Geological Department of the Hunterian Museum, Glasgow University, III.*
By J. Weir (with descriptions of Echinoidea by Ethel D. Currie, and of Corals by Mary Latham). *Jackson, Wylie and Co.*
12 s. 6d. 9¾ x 12¼; 63 + 5 plates *Glasgow*

This monograph contains the following sections: "The Jurassic geology of British Somaliland," "The geology of the Juba and Daua Rivers," "The Marehan Sandstone," "The palaeontology of the Jurassic Rocks described in Mr. Glenday's Report," "Description of the fossils—Mollusca, Brachiopoda, Echinoidea, and Corals," and a "List of the Fossils described." There is a list of 47 references and a group of excellent photographic plates.

NEW VIEWS ON EVOLUTION.
By George P. Conger. *The Macmillan Co.*
$2.50 5⅜ x 7¾; ix + 235 *New York*

This volume of the *Philosophy for the Layman* Series treats of the concept of evolution, not only in biology, but in physics, chemistry, geology, psychology and sociology. The conclusion reached

is that, while there is no decisive evidence against creationism, evolutionism is a valuable correlating principle.

THE EVOLUTION OF EARTH AND MAN.
By L. L. Woodruff, G. H. Parker, R. S. Lull, Charles Schuchert, H. B. Ferris, Joseph Barrell, A. G. Keller, G. G. MacCurdy, Ellsworth Huntington, J. R. Angell, E. G. Conklin, W. R. Coe. Edited, with a Preface, by George A. Baitsell.
Yale University Press
$5.00 6 x 9; xv + 476 *New Haven*

This is a revised edition of *The Evolution of the Earth and Its Inhabitants* and *The Evolution of Man* combined into one volume. Two new chapters have been added: Cultural Evolution, by G. G. MacCurdy, and the Mechanism of Evolution, by W. R. Coe. These additions live up to the high standard of the original chapters.

DUST TO LIFE. *The Scientific Story of Creation.*
By Burton P. Thom. *E. P. Dutton and Co.*
$5.00 $5\frac{3}{4}$ x $8\frac{5}{8}$; xv + 409 *New York*

A popular account of evolution, which, after a couple of introductory chapters on cosmogeny, devotes itself with considerable thoroughness to a setting forth of the results of paleontology, ending with an account of the ascent of man. The book is entertainingly written, and abundantly illustrated with line drawings. It lacks any bibliography, but is well indexed.

ORGANIC EVOLUTION.
By Richard S. Lull. *The Macmillan Co.*
$4.50 $5\frac{1}{2}$ x $8\frac{1}{2}$; xix + 743 *New York*

A revised edition of a well known text book.

SECOND BIBLIOGRAPHY AND CATALOGUE OF THE FOSSIL VERTEBRATA OF NORTH AMERICA.
Carnegie Institution of Washington Publication No. 390, Vol. 1.
By O. P. Hay.
Carnegie Institution of Washington
$7.50 (paper) *Washington*
$8.50 (cloth)
$6\frac{1}{4}$ x 10; viii + 916

Supplementary to a similar volume issued in 1902, and covering the literature published subsequent to that dealt with in the first work.

GENETICS

BESTIMMUNG UND VERERBUNG DES GESCHLECHTS BEI TIEREN. *Handbuch der Vererbungswissenschaft, Lieferung 10.*
By Emil Witschi. *Gebrüder Borntraeger*
10 marks (paper) *Berlin*
20 marks (bound)
7 x $10\frac{1}{2}$; 115

DAUERMODIFIKATIONEN. *Handbuch der Vererbungswissenschaft. Lieferung 11.*
By J. Hämmerling. *Gebrüder Borntraeger*
6 marks (paper) *Berlin*
12 marks (cloth)
7 x $10\frac{1}{2}$; 69

These two new parts of the Baur-Hartmann handbook of genetics furnish useful summaries of the literature of sex determination in animals and permanent modifications of unicellular organisms. Witschi's contribution devotes approximately 100 pages to primary sex determination, under two main headings, genetic analysis, and the physiology of primary sex determination. Hämmerling reviews the literature of *Dauermodifikationen* in *Paramecium, Arcella, Gonium,* and a few other organ-

isms. Both parts carry extensive, though by no means exhaustive, bibliographies.

HEREDITY IN MAN.
By R. Ruggles Gates. *The Macmillan Co.*
$6.00 5⅝ x 8¾; xiii + 385 *New York*

This volume began as a new edition of Professor Gates' earlier book on heredity and eugenics, and ended as what practically amounts to a new and different book, under a new title. In its present form it is one of the most useful summaries of the present state of knowledge regarding human inheritance which has come to our attention. It covers the field systematically and thoroughly. The bibliography, arranged by subjects, chapter by chapter, is extensive, and complete enough for all practical purposes of a handbook. Professor Gates merits the congratulations of all students of human biology for the book.

BLOOD GROUPING IN RELATION TO CLINICAL AND LEGAL MEDICINE.
By Laurence H. Snyder
The Williams & Wilkins Co.
$5.00 5⅞ x 9; xi + 153 *Baltimore*

In this book are to be found all the important developments of the many phases of the problem of blood grouping. The author, who has had much practical experience in performing transfusions in addition to having been an experimentalist, particularly in the field of inheritance of blood groups, their racial distribution, and pathological and physiological conditions, is well fitted to prepare such a treatise. It will be highly useful to both the legal and medical profession and invaluable to the research worker. The volume contains numerous tables and diagrams, an extensive bibliography and an index.

GENERAL BIOLOGY

BIOLOGICAL PRINCIPLES. *A Critical Study.*
By J. H. Woodger. *Harcourt, Brace and Co.*
$7.00 5⅜ x 8½; xii + 498 *New York*

There has been in the last fifteen years, largely as a result of developments in the new physics, a renaissance of interest in the philosophy of science, and to an important degree it affects the outlook of biology. The biologist can no longer take his fundamental viewpoint from the simple mechanism of the text book of physics, if for no other reason, because physicists have abandoned this view as inadequate to their own phenomena. Interestingly enough, the modification of the philosophy of mechanics is in the direction of an organic idealogy. There is a distinct need now, for a probing of biological fundamentals by biologists, to align their viewpoint with that of their fellows in the search of knowledge. Towards that end, the present work is a significant and welcome contribution. The author, who is a reader in biology in the University of London, painstakingly surveys *seriatim*, the various important philosophical viewpoints that affect biology, and critically examines their logical and epistemological content. His own views, some of which have been presented in The Quarterly Review of Biology, are well worth considerable attention but lack of space will not permit an adequate statement of them. Suffice it to recommend the book as probably the best review extant of biological philosophy in its current important aspects.

L'ORDINE DEI TEMPI E DELLE FORME IN NATURA. *Introduzione allo Studio Generale delle Funzioni Periodiche. In two parts.*
By Vincenzo Capparelli. *Licinio Cappelli*

100 lire *Bologna*
7 x 10; Part I, 258 (paper)
Part II, 533 (paper)

This extensive and detailed critical review of what is known about cyclical phenomena in the biological realm is a valuable addition to general biological literature. The first volume is historical, and discusses the various theories of the rhythms and cycles which have been advanced by biologists, medical men, and philosophers. The second volume reviews the recent as well as the ancient literature of biology relative to such matters as seasonal periodicity of morbidity and mortality, growth, reproduction, etc. The treatise is well documented and illustrated. The lack of an index unfortunately impairs greatly its usefulness as a reference work.

OUTLINES OF MODERN BIOLOGY.
By Charles R. Plunkett.
Henry Holt and Co., Inc.
$3.75 5⅜ x 8½; vii + 711 *New York*

This generation sees biologists who are no longer natural historians or morphologists representative of the older school but instead are chemists and physicists of living matter, albeit still teaching their subject largely from texts mostly based on the older discipline. It has not been uncommon for teachers of biology to regard their field as somehow being more difficult for students than that of other sciences, and possibly this impression is reflected by the less stimulating character of many collegiate texts published in the past. In the present work, however, the author's aggressive attitude toward modernizing collegiate biology is expressed by his statement that his book is no more difficult than modern college textbooks of physics and chemistry, and that he perceives no good reason why they should be less so, in view of the greater inherent complexity of the subject matter of biology. Progressive teachers of biology will unquestionably be in sympathy with this attitude.

Dr. Plunkett builds his book around the concept of the living organism as a physico-chemical mechanism, the emphasis being on general principles rather than on the factual details one associates with a text written from the basis of the type system. The initial theme of protoplasm is amplified into sections dealing with the comparative physiology of plants and animals under the headings of nutrition, response, reproduction, and evolution. The many still unanswered questions of biology are not ignored but viewed as stimulating problems rather than discouraging mysteries. A thoughtful chapter on the origin and nature of life concludes the volume, while his last statement crystallizes the central problem of biology today—that the essential "secret of life" lies in the genes themselves; their composition and structure, how they are autocatalytically synthesized, and how they may have first originated from lifeless matter.

Not only has the author given us a useful and tested text but it is highly probable that it is pioneer to others of similar but more detailed plan. It is to be especially recommended for the use of students who have had some previous training in science.

LES ULTRAVIRUS ET LES FORMES FILTRANTES DES MICROBES.
By Paul Hauduroy. *Masson et Cie*
40 francs 6⅛ x 9¼; 392 (paper) *Paris*

Bacteriologists should all be grateful to Dr. Hauduroy for getting together in one place an enormous amount of information on a subject which is now an exceedingly important and interesting one. One hundred and fifty-five titles are listed in the

bibliography and many more are scattered throughout the text. Hauduroy discusses the ultraviruses which attack not only man but plants, bacteria, insects, fishes, birds, and mammals. He discusses the recent discoveries which make it appear almost certain that there is a filtrable form of the virus of tuberculosis. The book is well written and the material is arranged in an orderly way. It should make a valuable addition to the library of every bacteriologist.

MY TROPICAL AIR CASTLE. *Nature Studies in Panama.*
By Frank M. Chapman.
D. Appleton and Co.
$5.00 5¾ x 8¾; xv + 415 *New York*

This is an extremely interesting and entertaining book about Barro Colorado, an island in Gatun Lake in the Panama Canal Zone, and the research laboratory on it. While written primarily for the general public every biologist, whether he has worked at Barro Colorado or hasn't, will enjoy reading it. Naturally the avian fauna gets the major part of the space, but no part of the extraordinarily rich life of the island is wholly neglected. The volume is extensively and beautifully illustrated by photographs and drawings. It is popular natural history at its very best.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 309. Methoden der Süsswasserbiologie.* Containing following articles: *Anleitung zur Untersuchung des Limnoneustons*, by W. M. Rylov; *Haltung und Aufzucht von Süsswasserbryozoen*, by Heinz Graupner; *Die Zucht des Phytoplanktons, Die Zucht von Cladoceren, eines Ostracodens, von Copepoden und planktischen Rotatorien*, and *Die Zucht des Aufwuchses unter Anwendung der Methode des Aufwuchsträgers*, by Einar Naumann; *Methoden der teichwirtschaftlichen Versuchsanstellung*, by Reinhard Demoll and Emil Walter; *Die Messung des Eindringens von Licht in Wasser mit photoelektrischen Zellen*, by V. E. Shelford; *Methoden zur Untersuchung von Flusslebensgemeinschaften*, by V. E. Shelford and Samuel Eddy.
Urban und Schwarzenberg
9 marks 7 x 10; 165 (paper) *Berlin*

This number of the Abderhalden Handbook deals with methods of fresh water biology. Among the most generally interesting of the papers are those of Rylov on the organisms of the surface scum of stagnant pools, of Shelford on the measurement of the penetration of light into water, and of Shelford and Eddy on the ecology of rivers.

NATURE NARRATIVES. *Volume I.*
By Austin H. Clark.
The Williams & Wilkins Co.
$1.00 4⅞ x 7¼; viii + 135 *Baltimore*

Dr. Clark has the great advantage over many of his fellow popularizers of science of knowing what he is talking about. These articles, originally written for a newspaper syndicate, are convincing evidence that accuracy and picturesqueness are not necessarily incompatible.

BACKGROUNDS OF BIOLOGY.
By John Giesen and Thomas L. Malumphy.
The Bruce Publishing Co.
$2.50 5½ x 8½; x + 278 *Milwaukee*

Two professors in a Roman Catholic college give in this book an introduction to biology for those students who have not time for a more extended course. In their treatment of evolution they are careful to

give the Darwinian dogs the worst of the argument.

INSTRUCTIONAL TESTS IN BIOLOGY. *Comprising Twenty-five Tests in Animal, Human, ana Plant Biology for Junior and Senior High Schools.*
By J. G. Blaisdell. *World Book Co.*
32 cents *Yonkers-on-Hudson, N. Y.*
6 x 10; viii + 56 (paper)

HUMAN BIOLOGY

QUESTIONED DOCUMENTS. *Second Edition.*
By Albert S. Osborn (with an Introduction by Prof. John Henry Wigmore).
The Boyd Printing Co.
$12.50 $6\frac{1}{4}$ x $9\frac{1}{4}$; xxiv + 1028 *Albany*

The author of this stately and beautifully printed volume is an outstanding expert on handwriting, and, in this revised edition of what has long been a standard treatise, has produced probably the best work on the subject now in existence. As the title indicates the primary viewpoint is legalistic, that of the handwriting expert in the courtroom. But this point of view, because of its very detachment, probably adds to rather than detracts from the usefulness and interest of the book to the human biologist. Handwriting has been far too much neglected by the human biologists in general, and the anthropologists and psychologists in particular. They have left the field too much to quacks and charlatans. The handwriting of an individual is a highly stable, objective and quantitatively measurable personal characteristic, which, in a sense, integrates a whole series of extremely delicate and complex individual differences in the physiology of nerve and muscle.

In this volume Mr. Osborn furnishes a sound, clear, and detailed basis for anyone who is interested in the scientific study of handwriting. He has devised measuring instruments adapted to such study, and has thoroughly done a lot of the inevitably necessary spade work which must underlie every really scientific approach to the problems of handwriting. His book is itself, in the highest sense, a scientific treatise. In an earlier work, *The Problem of Proof*, which, by the way, every scientific man will find interesting and valuable reading, Mr. Osborn made clear his possession of the scientific mentality and outlook. The present book should be in every anthropological, psychological, and, indeed, general biological library. It is extensively illustrated, meticulously documented, and indexed in detail.

ETHNOGRAPHY.
By Loomis Havemeyer. *Ginn and Co.*
$4.80 6 x $9\frac{1}{8}$; vi + 522 *Boston*

This is a compilation of ethnographic material, from well known sources, for use as an elementary text. The author specifically disclaims any originality of material. Sixteen chapters of the book were privately printed ten years ago, and have been used successfully in the author's classes at Yale since. There are five general sections, dealing respectively with the black, brown, red, yellow, and white races. Blacks and reds get the bulk of the space. Under the yellow race only Tibetans and Yakuts are discussed, and under the white race only Hindus. The author excuses the obviously large omissions on the ground that there is not space enough in an elementary text of this sort to treat all divisions of mankind. The author states that the book

is supposed to supply a set of facts drawn from the most reliable sources upon which the development of

a science of society may rest. I have excluded everything that is not a matter of agreement on the part of nearly all competent authorities. These facts I have not attempted to interpret, leaving matters of that sort to the discretion of the reader.

The book is abundantly and well illustrated, and within its self-imposed limitations is an excellent textbook for college and university classes.

THE DAWN OF A NEW CIVILIZATION.

By Hardy Wilson. *Cecil Palmer*
7 s. 6 d. 5 x 7⅜; 288 *London*

This curious book, cast in the guise of fiction, and in manner falling somewhere between the *Education of Henry Adams* and H. G. Wells at his theological worst, makes a highly futile Australian architect travel about the world and be dissatisfied with architecture and art in general. The basic thesis appears to be to the effect that

All signs show that we have arrived at one of those great changes when mankind moves from one period of creativeness, which has come to an end, towards another, which has not yet appeared. This period of transition means trials and failures before success is accomplished. The desire for creativeness is universal.

So far as is known creative men, in all ages, never were more than a few, and their lead was followed because of an instinctive desire to follow creativeness which affects everything about a race. Throughout periods of history it was a ruling force, and now it has reached, or is reaching, the end of a period, and so man turns to a new awakening. His creativeness always has occurred, in the first place, within that belt where the influence of the sun is dominant. Apparently, the perception of new creativeness is impossible outside of the belt, which is without white people who have energy and power to conceive a new period of civilization, unless it can be started in the southern United States, or Italians move southwards, and contact is established with China, or wherever inspiration may be found. As geographical position has been the determining factor in old moves, it is more likely that the United States will establish creative contact with the Chinese.

The book contains a dreadful libel on Richmond, Virginia, and some other odd information (?) about Maryland and Virginia, amongst which the following is a gem: "Jefferson Jackson's house, at Charlottesville, was a charming place too, and stood amongst leafy trees, smiling on a hill."

CRIME, DEGENERACY AND IMMIGRATION. *Their Interrelations and Interreactions.*

By David A. Orebaugh. *Richard G. Badger*
$3.00 5⅛ x 7½; xvi + 272 *Boston*

The author says in the preface of this book that "a cursory perusal of the book will disclose to the most unsophisticated that it was not written for the scientist, or expert in criminology." Possibly that is the reason why he has such smooth sailing in defending the following points:

Degeneracy, a form of retrogressive evolution having its basis in evil heredity, predisposes to crime and may in fact be said to be its chief cause.

The extreme prevalence and increase of crime in America furnishes conclusive proof that degeneracy is widespread and increasing.

Crime and degeneracy as concurrent and mutually related phenomena in our social and civic life became unduly manifest and continued to increase both in volume and flagrancy contemporaneously with and in direct ratio to the immigration of low grade southern and eastern Europeans.

By the intermixture, both racially and socially, of the disharmonic and intellectually inferior element referred to with the old American stock, the racial blood-stream of the latter has been corrupted and degeneracy in varying degrees has supervened.

A consideration of all of the factors mentioned leads to the conclusion that the way to abolish or diminish crime is to eradicate degeneracy. The relation of crime to degeneracy, or degeneracy to immigration, and the reaction of each upon the other is readily discernible upon examination.

STUDIES IN THE NATURE OF CHARACTER. *By the Character Education In-*

quiry, Teachers College, Columbia University, in Coöperation with The Institute of Social and Religious Research. II. Studies in Service and Self-Control.

By Hugh Hartshorne, Mark A. May, and Julius B. Maller. *The Macmillan Co.*

$2.75 5⅛ x 7¾; xxiii + 559 *New York*

In this volume the authors pass from the statistical study of deceit to that of altruism and self-control. In all three cases they have found "evidence for doubting the efficacy of certain conventional efforts at character development in both secular and religious circles." Apparently they are somewhat surprised to find that in unselfishness, as in height or weight, the distribution is not bimodal.

STUDIES IN THE COMPARATIVE ABILITIES OF WHITES AND NEGROES. *Mental Measurement Monographs Serial No. 5.*

By Joseph Peterson and Lyle H. Lanier.

The Williams & Wilkins Co.

$5.00 6 x 9; vi + 156 (paper) *Baltimore*

The outstanding result of our tests of adults is an enormous and reliable superiority of whites over negroes in all four group intelligence tests, this being true of the wholly non-verbal International rotator tests as well as of the Binet group, the Myers, and the Atkinson test. No sex differences in these tests are established.

In view of various sorts of evidence of effects of "cultural sets" on efficiency in different tests, effects which vary considerably from test to test, it is well to consider the question as to the degree of innateness of the racial differences here found an open one, though evidence points to a difference in native intellectual ability favoring the whites.

SOCIOLOGY AND SIN. *A Plea for the Exclusion of Uplift from Economics and the Political Sciences.*

By P. Sargant Florence.

W. W. Norton and Co., Inc.

$1.00 4⅛ x 6½; 98 *New York*

The author wishes very strongly that sociology be pursued in the indicative, not the optative mood. It should concern itself with the careful and exhaustive study of things as they are and eschew the expression of how things ought to be. Then others, who should make it their specialty to envisage the ideals of society, can utilize the disinterestedly established truths for whatever ends they deem worthy.

THE HEALTH OF WORKERS IN DUSTY TRADES. *II. Exposure to Siliceous Dust (Granite Industry). Public Health Bulletin No. 187.*

By A. E. Russell, R. H. Britten, L. R. Thompson, J. J. Bloomfield (with sections on autopsy material by L. U. Gardner and on silica by A. Knopf).

U. S. Government Printing Office

$1.15 *Washington*

5¾ x 9⅛; iv + 206 (paper)

This bulletin, the second in an important series of investigations dealing with the health of individuals whose labors are in the so-called dusty trades, deals with a study of "silica dust of a definitely known composition in its effect on the health of the workers." Some of the salient points of this report are:

(a) The long period of service before the liability to tuberculosis becomes manifest (generally 20 years or more). (b) The sharp correlation between length of exposure to the dust and prevalence of tuberculosis and also the death rate from this disease. (c) The close relation between extent of dust exposure and health of the men. (d) The universal occurrence of silicosis among the workers. (e) The large proportion of workers finally succumbing to tuberculosis. (f) The almost invariably fatal form of the disease within a short time after the onset. (g) The different character of silicosis as manifested by X-rays compared with that shown where there is exposure to a dust with a much higher content of free silica. (h) The location of the tuberculous lesion, usually basal, where the disease complicates silicosis. (i) The absence of deaths from silicosis per se, tuberculosis ap-

parently always intervening. (j) The failure of workers to recover from their condition upon going into nondusty trades. (k) The high incidence of sickness of a severe nature from causes other than tuberculosis. (l) The rising sickness and mortality rates from tuberculosis due to longer use of the hand pneumatic tool. (m) The appallingly high death rates at the present time from tuberculosis, compared with normal industrial experience.

Many of the case histories are reported together with x-ray pictures of the chests of the individuals. A large number of tables and figures are included in the text. Unfortunately there is no index.

GENIALE MENSCHEN.
By Ernst Kretschmer. *Julius Springer*
12 marks (paper) *Berlin*
15 marks (cloth)
$6\frac{3}{8}$ x $9\frac{1}{2}$; vii + 254

This volume is an interesting study of the personality (in the technical sense of modern constitutional research) of men of genius, and the biology and psychology of the origin and development of genius, by an outstanding and acknowledged leader in the field. The book is stated to be a revision and expansion of lectures dating from 1919 and in part separately published. The final section is a collection of portraits of distinguished men. It appears that the great philosophers have been mainly leptosomal in habitus. Pyknics are extremely rare among them. On the other hand pyknics are in the majority among the distinguished biologists of the past, including medical men as well as zoölogists and botanists. There is no index, unfortunately.

THE CONQUEST OF THOUGHT BY INVENTION. *In the Mechanical State of the Future.*
By H. Stafford Hatfield.
W. W. Norton and Co., Inc.
$1.00 $4\frac{1}{4}$ x $6\frac{1}{2}$; 80 *New York*

The author, a successful inventor himself, apparently has considerable personal distaste for the automatism of life brought in by the machine, and its consequence, the suppression of individuality. But generally there is no opposition to this tendency. Most persons prefer security to the opportunity for self expression, and the whole tendency of physical, social, and political forces is in the direction of the State taking on the guidance of living. He looks toward the time when the white races

will settle down to live in a manner closely analogous to that of other routinized organisms such as ants and bees, and initiative will be withdrawn from society at large and most likely die out more or less rapidly. All this is happening, so it seems to me, in so inevitable a manner that any argument concerning its desirability appears futile.

MAN'S GREAT ADVENTURE. (*Thirty Stories of Mankind from the Dawn Man to the Man of To-day*).
By Stephen Southwold.
Longmans, Green and Co.
$1.75 $5\frac{1}{4}$ x $7\frac{1}{4}$; 256 *New York*

This is an outline of history for boys of ten, written in the form of short stories attempting to typify the great human movements of the various periods from the Old Stone Age down to the present day. The aim of the author is to make his young readers realize, first, that the people of Rome, Greece, and Babylon were really human beings, and second, that Sherman spoke the truth about war. It is written that the good bishop Ulfilas, when he was translating the Scriptures into Gothic, left out the books of Kings because he feared the bad effect of so much fighting on his brother Goths. Now there is a good deal of the Goth in the average boy of ten; we fear that what will impress him in this book will be, not the suffering and cruelty of war, but the glamor of fighting.

FRANÇOIS RABELAIS. *Man of the Renaissance. A Spiritual Biography.*
By Samuel Putnam.
Jonathan Cape and Harrison Smith
$3.50 5¾ x 8¾; xiii + 530 *New York*

Rabelais is one of the great legends of literary history. Read comparatively little, his name at least is known to all and Rabelaisian cults of one sort or another abound. He is known variously as a retailer of smutty stories (thanks to our Postoffice Department), a jolly winebibber, a devotee of the dissolute life and the belly, an irresponsible humorist, a great romancer. The author rescues his subject from the confusing enthusiasts and portrays him for what he primarily was, a great scholar, albeit humorous, literary, and coarse as befitted his time of the Renaissance. Mr. Putnam is one of America's greatest authorities on Rabelais and much learning goes into the book. But it is not pedantic and is never dull.

MAN'S PLACE AMONG THE MAMMALS.
By Frederic Wood Jones.
Longmans, Green and Co.
$7.50 5½ x 8½; xi + 372 *New York*

Students of biological literature are already acquainted with the general thesis of this book: namely, that man must seek his ancestors not among the apes and monkeys but among the primitive *Tarsius*-like animals. A number of years ago the author first published his investigation on the origin of man. At that time his work received much adverse criticism. In this volume we have a restatement of the subject and one is inclined to think that the criticisms will be somewhat less severe, even if there are many who cannot follow the author all the way. In any event, at a time when the monkeys and apes are so much under fire there seems to be much offered in these pages which cannot be ignored in a search for our fore-fathers.

MAN AND WOMAN. *A Study of Secondary and Tertiary Sexual Characters.*
By Havelock Ellis. *Houghton Mifflin Co.*
$5.00 5½ x 8⅛; vii + 495 *Boston*

This edition is Ellis' well known book "remoulded and put into more popular form." The change involves some additions and some omissions from the earlier issues. In some ways we prefer the more original form, as represented for instance in the 6th edition previously noted in these columns.

GRUNDPROBLEME DER KONSTITUTIONSFORSCHUNG. *Würzburger Abhandlungen aus dem Gesamtgebiet der Medizin Band VI, Heft 3.*
By Hans Günther. *Curt Kabitzsch*
2 marks 6⅝ x 9½; 23 (paper) *Leipzig*

This *Antrittsvorlesung* delivered at the University of Leipsic is an interesting and valuable contribution to the literature of constitution studies. Its purpose is to examine critically the underlying concept of this branch of human biology. The need for such a philosophical examination of the case is well shown by the accompanying bibliography, in which every entry is accompanied by a quotation of the cited author's conception of what "constitution" means. It is plain that there is not yet any general agreement regarding fundamentals in this field.

THE WAY OF THE SEA. *The Corridors of Time VI.*
By Harold Peake and Herbert J. Fleure.
Yale University Press
$2.00 5½ x 8⅛; viii + 168 *New Haven*

This volume of *The Corridors of Time* carries the story of man's early development through the period from 2100 to 1600 B.C. The authors conclude that the megalithic monuments do not date from remote prehistoric periods, but are the result of intercourse with the eastern Mediterranean not long before 2000 B.C.

TEMPERANCE OR PROHIBITION? *The Hearst Temperance Contest Committee, Francis J. Tietsort, Editor*

$1.00 *220 South St., New York* 5 x 7⅜; xxii + 397

An epitome of the plans submitted in the contest conducted by the Hearst newspapers for a substitute for the present attempt at prohibition. The winning plan suggests the repeal of the Volstead act and the substitution for it of a law "defining the words 'intoxicating liquors' as 'all alcoholic products of distillation.'"

WOMEN IN GAINFUL OCCUPATIONS 1870 TO 1920. *A Study of the Trend of Recent Changes in the Numbers, Occupational Distribution, and Family Relationships of Women Reported in the Census as Following a Gainful Occupation. Census Monographs IX. By Joseph A. Hill.*

U. S. Government Printing Office

$1.50 7 x 10; xvi + 416 *Washington*

This monograph deals not only with the general census tabulations for gainfully occupied women but also with a special study of the family relationships of gainfully occupied women in eleven selected cities. In view of the heated discussions of the wage-earning married woman that one often hears, it is interesting to note that only 9 per cent of the married women in the United States are wage-earners.

MAGIC SPADES. *The Romance of Archaeology. By R. V. D. Magoffin and Emily C. Davis.*

Henry Holt and Co.

$5.00 6 x 9¼; xv + 348 *New York*

This book certainly succeeds in its intention of proving to the general reader that archaeology is a fascinating study. Professor Magoffin tells the story of modern discoveries in the Mediterranean region and Mesopotamia; Miss Davis deals with Britain, Scandinavia and America. Both show how interesting the reconstruction of a past era from its buried remains may be.

MEDICAL LEADERS *from Hippocrates to Osler. By Samuel W. Lambert and George M. Goodwin.* *The Bobbs-Merrill Co.*

$5.00 5¾ x 8¾; viii + 331 *Indianapolis*

The non-medical reader will find in this book an excellent account of the history of medicine, correlated with the general intellectual development of the various periods. There is an abundance of picturesque detail in the narrative.

CAUSES AND PREVENTION OF NEONATAL MORTALITY. *United States Department of Labor. Children's Bureau. By Richard A. Bolt.*

U. S. Government Printing Office

5 cents 5½ x 9¼; 18 (paper) *Washington*

PREVENTION OF NEONATAL MORTALITY FROM THE OBSTETRICIAN'S POINT OF VIEW. *United States Department of Labor. Children's Bureau. By Fred L. Adair.*

U. S. Government Printing Office

5 cents 5½ x 9¼; 9 (paper) *Washington*

ANALYSIS AND TABULAR SUMMARY RELATING TO JURISDICTION IN CHILDREN'S CASES AND CASES OF DOMESTIC RELATIONS IN THE UNITED STATES. *U. S. Department of Labor, Children's Bureau, Chart No. 17.*
By Freda Ring Lyman.
U. S. Government Printing Office
10 cents *Washington*
9 x 11¼; v + 33 (paper)

ZOOLOGY

INSECTS, TICKS, MITES AND VENOMOUS ANIMALS *of Medical and Veterinary Importance. Part I. Medical.*
By Walter S. Patton and Alwen M. Evans.
Entomological Department, Liverpool School of Tropical Medicine
20 shillings 7 x 9⅝; x + 786 *Liverpool*

This book replaces Patton and Cragg's *Textbook of Medical Entomology* which is now out of print. It forms the first of a series of four parts, each complete in itself. Although prepared primarily for the medical officer approaching the subject for the first time it will be of much use to the student of general and agricultural entomology, and invaluable to the medical officer in isolated tropical regions whose library is necessarily limited. Much space has been devoted to morphology and phylogeny, while very full notes are given on the early stages, bionomics and relation to disease of all the insects and Acari of medical importance. Included also is a great deal of more detailed information which at present is not available in entomological books or papers. The introductory section is followed by five sections devoted to the study of the external and internal anatomy of an arthropod, the Diptera being used largely as types. The remaining sections, twenty-two in all, are devoted to the systematic part of the course.

The book is beautifully illustrated with numerous photographs and drawings, mostly original. There is an excellent index but no list of references. A large sheet at the end of the book gives an illustrated key to the scheme of classification of the arthropods.

ANIMALS LOOKING AT YOU.
By Paul Eipper. *The Viking Press*
$3.00 6 x 9¼; 163 *New York*

A fascinating book which will appeal to all animal lovers. The author, an almost daily frequenter of zoological gardens for 35 years, gives, in numerous brief sketches, some of his experiences with animals kept in captivity. In doing so, without attempting in any way to interpret the varied behavior of these animals, he succeeds in conveying to the reader a remarkably clear picture of the divergent personalities with which he was acquainted. He makes two pleas for animals kept in captivity—first, that there be sufficient space for each animal to permit of a reasonable amount of exercise, and, second, that there always be two of a kind kept together to relieve the dreadful fate of loneliness.

The song of the Orang, which gave him the most tremendous experience that he had ever had among animals, he describes as follows:

I had to wait for hours, but at last as the darkness set in, and shortly before Goliath retired to his sleeping chamber, it came to pass. Aw—Aw—Aw, soft and dull but very quick, like the pulsing of a motor. For ten seconds it came beating without pause from his throat, and was then broken by a sighing, sobbing intake of breath, and then swelled out again, this time an octave higher, and in a strong crescendo. Again a sigh and the Aw—Aw—Aw burst forth again, on a higher note than ever. The cry beat painfully against my ear-drums, and I saw how swollen was the Orang's throat pouch; and now mingled with the singing came a thunderous nerve-racking long-drawn-out H-u-u-u-

u-h. The mighty song resounded in powerful alternations, Aw—Aw—Aw—H-u-u-uh, as tremendous as the lions' roar. It was the song of primitive life, the thunderous speech of nature.

He tells of two giraffes tamed by a hunter and led hundreds of miles through African wilderness and over a high mountain range; of the white mouse and the venomous snake who dwelt amicably together although other mice were instantly devoured when put in the cage with the snake; of days spent with a group of orang-outangs—44 in number—in an acclimatization camp in southern France and of a trip from this camp to Berlin accompanied by a four year old gorilla and a young chimpanzee.

The book is illustrated with a group of very fine photographs, the most appealing perhaps being those of the orangs.

A NEW RODENT FROM THE GALAPAGOS ISLANDS. *Publication 261.*
By Wilfred H. Osgood.
Field Museum of Natural History
75 cents 6¼ x 9½; 4 (paper) *Chicago*

This makes the fourth or fifth rodent found on the islands, the first having been discovered by Charles Darwin, during his famous visit. It is called *Nesoryzomys darwini*. "With the addition of *N. darwini* to the other forms above mentioned, the rodents of the islands take on considerably more importance than formerly and will doubtless need serious consideration in speculation regarding the derivation of the insular fauna."

ANNOTATED BIBLIOGRAPHY OF THE MOSS MITES (*Oribatoidea, Acarina*). *By Arthur Paul Jacot.*
Catholic Mission Press
50 cents 5⅝ x 8½; 60 (paper) *Tsingtao.*

This annotated bibliography of the moss mites, chronologically arranged, is in three sections. In the first part the author places all the contributions which embody original material, these being grouped as follows: Eighteenth century; Early writers (to 1875); Italian and English era (1876–1894); American and Dutch era (1895–1904); Italian recrudescence (1905–1912); English recrudescence (1913–1919); German recrudescence (1920–). The other two sections of the bibliography contain miscellaneous comparative references, and compendiums, texts, translations and relists.

HALIOTIS. *Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals. XXIX.*
By Doris R. Crofts.
The University Press of Liverpool
10 s. 6 d. *Liverpool*
6 x 9½; viii + 174 + 8 plates (paper)

Aside from its interest biologically, *Haliotis* is of considerable economic importance, the shells being widely used in ornamentation, while there are several edible forms which form the basis of a thriving industry in California and Japan. The author of this book has brought together widely scattered material on the group of molluscs to which *Haliotis* belongs, many doubtful points have been cleared up, and much new material is contributed in the field of bionomics, cytology and physiology. Included in the work are 31 text-figures and 39 plates. There is a literature list of 69 titles.

A HANDBOOK OF THE MOSQUITOES OF NORTH AMERICA. *Their Structure, How They Live, How They Carry Disease, How They May be Studied, How They May Be Controlled, How They May Be Identified.*

By Robert Matheson. *Charles C. Thomas*
$5.50 6 x 9; xvii + 268 *Springfield, Ill.*
A simple, clear succinct account.

GENERAL CATALOGUE OF THE HEMIPTERA. *Fascicle II. Mesoveliidae.* *By Géza Horváth.* *Smith College*
50 cents *Northampton, Mass.*
6 x 9; 15 (paper)

GENERAL CATALOGUE OF THE HEMIPTERA. *Fascicle III. Pyrrhocoridae.* *By Roland F. Hussey, with Bibliography by Elizabeth Sherman.* *Smith College*
$1.50 *Northampton, Mass.*
6⅛ x 9; 144 (paper)

KEY-CATALOGUE OF PARASITES REPORTED FOR PRIMATES (MONKEYS AND LEMURS) WITH THEIR POSSIBLE PUBLIC HEALTH IMPORTANCE *by C. W. Stiles and Albert Hassall, and* KEY-CATALOGUE OF PRIMATES FOR WHICH PARASITES ARE REPORTED. *by C. W. Stiles and Mabelle Orleman Nolan. United States Treasury Department, Public Health Service, Hygienic Laboratory Bulletin No. 152.*
U. S. Government Printing Office
35 cents *Washington*
5¾ x 9⅛; iv + 192 (paper)

MORPHOLOGY AND DIVISION OF CHLAMYDOMONAS *with Reference to the Phylogeny of the Flagellate Neuromotor System. University of California Publications in Zoology, Vol. 33, No. 7.*
By J. McA. Kater.
University of California Press
60 cents *Berkeley*
7 x 10¾; 44 + 6 plates (paper)

BOTANY

MANGROVE FORESTS OF THE MALAY PENINSULA.
Malayan Forest Records No. 6.
By J. G. Watson.
Federated Malay States Government Conservator of Forests, Kuala Lumpur
$3.00 or 7 shillings post free

The mangrove forests or swamps of the Malay Peninsula cover an area of about 430 square miles. Of this area over 400 square miles have been constituted forest reserves. The principal species in these forests belong to four families, the Rhizophoraceae, Lythraceae, Verbenaceae, and Meliaceae. Subsidiary species fall in 15 families. The present volume is a detailed account of the general ecology of these forests, using the term "ecology" in the widest sense. It is extensively and beautifully illustrated with photographs, and will be of quite as great interest to the general botanist as to the student of forestry, for whom it was primarily written. It contains a bibliography of 55 titles and a detailed index.

STEPHEN HALES, D.D., F.R.S. *An Eighteenth Century Biography.*
By A. E. Clark-Kennedy.
The Macmillan Co.
$6.00 5½ x 8½; xii + 256 *New York*

In these days, when many of the clergy are actively hostile to science and the rest are more interested in reconciling it with theology than in understanding it, a clergyman who spent his spare time in scientific work would be looked on with astonishment and even, perhaps, with a certain disapprobation. In the eighteenth century men thought differently. There is no evidence that anyone felt that "the good Pastor Stephen Hales" sullied his cloth by his experiments on vegetable

statics, although Pope was squeamish over his vivisections. Those who wish to learn more about the work of a remarkable man will do well to read this book.

COAL MEASURE PLANTS.
By R. Crookall. *Longmans, Green and Co.*
$5.00 5¾ x 9; 80 + 39 plates *New York*
12 s. 6 d. *Edward Arnold and Co.*
London

This book deals with the external morphology of 240 of the more common and characteristic plants of the British Coal Measure. Brief descriptive notes are given in terminology easily comprehended by the amateur naturalist, but the author has in no sense made a popular field guide. Students of botany, geology and mining will find it an excellent introduction to paleobotany. The work includes numerous diagrams and line drawings and a group of excellent plates, also a list of species occurring in the book and an index.

OUR MOST POPULAR TREES.
By Lydia Northrop Gilbert.
George Sully and Co., Inc.
$1.50 4 x 6¾; 110 *New York*

A pocket guide for nature lovers, students and artists. It contains forty-eight full page illustrations in color, showing in detail the tree, bark, fruit, blossom and leaf.

LES LILIIFLORES DU QUÉBEC. (*Liliacées, Pontédériacées, Iridacées, Joncacées.*) *Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 14.*
By Frère Marie-Victorin.
Laboratory of Botany, University of Montreal
$1.50 6 x 9; 202 (paper) *Montreal*

ADDITIONS AUX CYPÉRACEES DE L'AMÉRIQUE DU NORD. *Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 15.*
By Frère Marie-Victorin.
Laboratory of Botany, University of Montreal
50 cents 6 x 9; 16 (paper) *Montreal*

VOCABULARY OF PLANT SOCIOLOGY.
By J. Braun-Blanquet and J. Pavillard. Translated by F. R. Bharucha.
F. R. Bharucha
1 shilling *Botany School, Cambridge*
6⅛ x 9½; 23 (paper)

MORPHOLOGY

THE CHROMOSOMES IN MAN: SEX AND SOMATIC. *Memoirs of the University of California, Volume 9, No. 1.*
By Herbert M. Evans and Olive Swezy.
University of California Press
$1.50 *Berkeley*
10 x 13; 41 + 11 plates (paper)

This short monograph summarizes briefly what has been done to date to elucidate the chromosomal organization in the cells of man. Most of it is occupied with a description of the original work of the authors. This is divided into investigations of the sex and somatic cells. For the former, there were utilized freshly preserved testicular material from six males, and for the latter sections from two embryos, from the uterus of a fifteen year negress, and from a carcinoma of the lip in a fifty-five year man. Definitive observations are recorded on the number of chromosomes, the differentiation into autosomes and X-Y chromosomes, the kinetics of the chromosomes during mitosis, and the mensuration of chromosomes. There are a considerable number of plates, reproducing chromosomal figures in large magnification.

TEXT-BOOK OF EMBRYOLOGY.
By F. R. Bailey and A. M. Miller.
William Wood and Co.
$7.00 6½ x 9¼; xvi + 687 *New York*

A fifth edition. While the general plan of the original text has been adhered to there has been much revision, particularly in the chapter on the nervous system. Parts of the book have been rewritten where recent investigations have modified the views expressed in the earlier editions. New figures have to some extent replaced old figures and new illustrations have been added.

THE ESSENTIALS OF HUMAN EMBRYOLOGY.
By Gideon S. Dodds.
John Wiley and Sons, Inc.
$4.00 5¾ x 9; vii + 316 *New York*

A textbook for medical and pre-medical students. Recognizing that there are many subjects besides embryology which the student must master, the author has tried to make his book as brief as is consistent with an adequate treatment. It is clearly and interestingly written and well illustrated and indexed.

PHYSIOLOGY AND PATHOLOGY

NOUVEAU TRAITÉ DE MÉDECINE.
Fascicule XVI. Pathologie du foie et des voies biliaires.
Chapters by various authors. *Masson et Cie*
125 francs 6⅜ x 9¾; viii + 1048 *Paris*

This volume represents a tremendous amount of work on the part of the several contributors. It is interestingly written and well illustrated, but it is very poorly bound. It is written largely from the point of view of the pathologist and the classifier of disease. The American reader today, who is perhaps more interested in trying to detect disturbances in liver function before the patient is bloated and hopelessly ill, will be somewhat disappointed because, so far as we can find, there is little or nothing about the practical use of the dye tests which are now so commonly employed. Similarly, there appears to be nothing about the icterus index or the van den Berg test, which has proved so helpful in the differentiation of the various types of jaundice. It is possible that these topics are discussed somewhere in the book, but if the reviewer missed them he does not feel as culpable as he would if there had been an index to help him in his search. The lack of interest in the physiologic aspects of liver disease is shown also by the absence of any reference to the work of Mann and his students, work which has thrown so much light on the functions of the liver.

It comes somewhat as a shock to see that the field of medicine has now become so enormous that it is possible to write a thousand pages on the diseases of one organ of the body. What is still more disturbing is the fact that these one thousand pages were not sufficient for the proper handling of the subject, and that many chapters have been left sketchy and inadequate, so far as the specialist is concerned. Much of the inadequacy must, of course, be ascribed to the fact that no one yet knows enough about the subject of liver function and liver disease, but some of it is due to the fact that no one man in any one part of the world can keep quite up to date, especially during the year or more in which he is swamped with the actual labor of writing a book.

And so we feel that any disappointment which a reviewer may feel at not finding

what he wants here and there, should not blind him to the fact that an enormous amount of useful information has been gathered in one place, and that the men who did the work deserve praise and many thanks from those whom they have served. And even if they have quarried mainly from the works of their own countrymen to the neglect of the writings of foreigners, let us take advantage of this human failing. Let Germans and Englishmen write similar texts in the same way and then we in America, by consulting three books on any one subject, can gain access to most of what is known in Europe on this subject. It may not be a bad thing for a student in America to learn that the discovery which he has always credited to Mann is ascribed by a French textbook writer, who never heard of Mann, to a Frenchman whom the American never heard of.

THE IMMUNOLOGY OF PARASITIC INFECTIONS.
By William H. Taliaferro.
The Century Co.
$6.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; xv + 414 *New York*

No better idea of the *raison d'être* of this important book can be given than by quoting from the preface where the author says:

> The present volume is not, in any sense, intended to be a treatise on immunology, but a compilation, and as far as possible, an evaluation of the mass of immunological work that has been done on infections with animal parasites. Besides stimulating interest in this field, I hope that the present work will hasten the incorporation of these experimental data into both parasitology and immunology, where, in spite of a growing interest during the past few years, it has been largely neglected. By achieving this, the parasitologist will undoubtedly gain new concepts for many of his experimental studies on infections, and the immunologist can obtain unique material for certain immunological questions.

The book has been especially arranged from the point of usefulness to student and investigator. Much pains has been taken to avoid confusion in nomenclature. The value of the book for reference purposes has been greatly enhanced by the lengthy literature list, the catalogue of parasites considered in the text and author and subject indices.

DIET AND EFFICIENCY. *A Five-Year Controlled Experiment on Man.*
By Harold H. G. Holck.
University of Chicago Press
$1.00 $5\frac{7}{8}$ x 9; viii + 72 (paper) *Chicago*

In the long and honorable list of men who have martyred themselves to the cause of scientific progress, the author of this little work certainly has a conspicuous place. For a total of about 525 days he subjected himself to the practice of *Fletcherizing*, i.e., thorough to excessive mastication of food taken only when actually hungry and stopped as soon as satisfied. What Brillat-Savarin or the more modern exponents of the art of the *gourmet* would say of such habits we shudder to think, but please remember Fletcher advocated his system for health, not happiness, which is another thing. A number of biochemical and physiological observations were made daily during the course of the experiment, and compared with the results of a normal control period. The conclusions of these extended investigations are that Fletcherizing decreased muscular endurance, typewriting accuracy and basal metabolism, had no significant effect on blood pressure, pulse, oral temperature, sleeping time, mental multiplication, and typewriting speed, improved efficiency in solving chess problems and the approach in body weight toward common standards.

LES ANOMALIES DU COMPLEXE VENTRICULAIRE ÉLECTRIQUE *Leur Importance en Clinique. (Essai d'Électro-Cardio-Pronostic.)*
By J. Robert Lévy. *Masson et Cie*
30 francs 6½ x 10; 202 (paper) *Paris*

Perhaps the greatest need of the cardiologist today is for more knowledge in regard to prognosis. Since the time of Imhotep the patient with heart disease has always been concerned most about his future: Is he going to drop dead? Must he hurry about making his will? Must he live as a valetudinarian, or can he drive at his business and at his golf ball as usual? Since these questions must be answered somehow it is a pleasure to find a book in which the prognosis of heart disease is based on the actual experience of the author, a man who has taken the trouble to follow up many of his patients to see how long they survived the discovery of their disease. Too many books are written by men who either haven't enough experience or who haven't the sense to rely on it. They haven't the vision to see that it is much more important and profitable to put down clearly that which they have seen and learned in the clinic and the laboratory than to rehash that which they have read in books. Although Dr. Levy writes largely from his own experience he refers also to over 400 articles written by other men working in all parts of the civilized world.

HOOKWORM DISEASE. *Its Distribution, Biology, Epidemiology, Pathology, Diagnosis, Treatment and Control.*
By Asa C. Chandler. *The Macmillan Co.*
$5.00 6⅛ x 9⅛; xii + 494 *New York*

A comprehensive treatise which will be invaluable as a general reference book to members of the medical profession as well as investigators. The author has brought together all of the important results which recent researches have revealed and has given to his readers much material which hitherto has not been easily attainable. The book contains a separate section devoted to "Technical Methods," a lengthy bibliography and an index.

PHYSIOPATHOLOGIE ET TRAITEMENT DU DIABÈTE SUCRÉ.
By H. Chabanier, M. Lebert and C. Lobo-Onell. *Masson et Cie*
50 francs 6½ x 10; 441 (paper) *Paris*

This book must be of considerable interest to students of diabetes because it contains so full a discussion of the threshold in kidney function which determines the point at which sugar accumulating in the blood flows over into the urine. We know of no other place in which the subject is so fully treated. Much research work is reported: work designed to show how the glycosuric threshold is influenced by the degree of glycemia, by the giving of insulin, and by other factors. The authors discuss also what they believe to be the basal defect in diabetes and the ways in which insulin affects this. This part of the book is not so valuable, however, because it is not up to date and does not appear to add much to the stock of knowledge on this point. The first half of the book is taken up with a discussion of the physiology of the disease and the second with problems of practical treatment. There are many references to the literature and there is a fair index.

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome VIII. Physiologie Musculaire Chaleur Animale.*
By Léon Binet, G. Bourguignon, P. Chailley-

Bert, J. Gautrelet, L. Lapicue, J. Lefèvre, R. Leriche, A. Policard, A. Strohl, G. Weiss.
95 francs (paper) *Masson et Cie*
110 francs (bound) $6\frac{5}{8}$ x $9\frac{1}{2}$; 742 *Paris*

Another volume in a comprehensive series on human physiology which has been previously noted in these columns. Contrary to the promise of the title, the portion devoted to pathological states is minimal; the references are meager and scattered, and the book has no general index. It does not compare favorably with the German series issued under the editorship of Bethe.

LE CŒUR. *Les Médicaments Cardiaques et l'Électrocardiogramme. Recherches Expérimentales du Laboratoire de Thérapeutique de l'Université de Liége.*
By F. Henrijean. *Masson et Cie*
50 francs *Paris*
$6\frac{1}{4}$ x 10; xxiv + 416 (paper)

The researches with which this volume deals were begun on the pharmacological problem of the mechanism of the action of drugs on the heart, a question which led to the more general problem of the nature of the heart action. The author concludes that the origin of the cardiac contractions is in neither the heart muscle nor the nerves, but in tissues which preserve the mixed character of the embryonic heart tissue, being both contractile and conductive.

NOUVEAU TRAITÉ DE MÉDECINE. *Fascicule V (Tome II). Le Cancer.*
By Gustave Roussy with the collaboration of Roger Leroux and Maurice Wolf.
Masson et Cie
100 francs *Paris*
$6\frac{1}{2}$ x $9\frac{3}{4}$; viii + 846

This is a revised edition, completely rewritten and considerably enlarged, of Dr. Roussy's cancer volume published in 1922 as a part of the *Nouveau Traité de Médecine*. In its present form it is one of the best general accounts of cancer available. Every aspect of the subject is discussed. The range and thoroughness of the work may be indicated by the statement that the bibliography, which includes only writings consulted or cited in the text, covers 69 closely printed, double column pages of small type. The volume is extensively and well illustrated, and altogether constitutes a reference work of first class importance and usefulness.

LE LIQUIDE CÉPHALO-RACHIDIEN. *Physiologie et Exploration du Système Ventriculo-Méningé.*
By Dr. Riser. *Masson et Cie*
28 francs $6\frac{1}{4}$ x $9\frac{5}{8}$; 250 (paper) *Paris*

The primary purpose of this interesting and useful volume is to give a well-rounded account of the important researches on the physiology of the cerebrospinal fluid which have been carried out in the *École Neurologique* at Toulouse during the last decade under the direction of Professor Cestan. The author formally disclaims any intention of making a systematic general review of knowledge regarding the cerebrospinal fluid. Instead it is especially devoted to a critical exposition of the various recent methods of exploration by the injection of air, colored solutions, lipiodol, etc., and their medico-surgical applications.

THE ESSENTIALS OF CHEMICAL PHYSIOLOGY *for the Use of Students.*
By W. D. Halliburton, J. A. Hewitt and W. Robson. *Longmans, Green and Co.*
$3.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; xii + 383 *New York*

The author of this well known text book has been assisted in the preparation of this, the twelfth, edition by two collaborators. The general scheme of the book is unchanged but there has been a rearrangement of the detailed material and the necessary additions made to bring the book up to date.

LE MÉTABOLISME BASAL.
By Marcel Labbé and H. Stévenin.
Masson et Cie
40 francs $6\frac{1}{8}$ x $9\frac{1}{4}$; 343 (paper) *Paris*

The authors have prepared a good systematic treatise on basal metabolism, one which will doubtless be of great assistance to the young Frenchman who takes up the study of the subject. It is doubtful if it will be of much interest to the American specialist except at such times as he is looking for references to the work of French investigators. As anyone can see by glancing at the names of the authors quoted throughout the book, Labbé and Stévenin had to depend on Americans for most of their information in regard to the clinical application of calorimetry.

PELADES ET ALOPÉCIES EN AIRES.
Les Syndromes Alopéciques V.
By R. Sabouraud. *Masson et Cie*
80 francs $6\frac{1}{2}$ x 10; 378 (paper) *Paris*

This, the last of the five monographs on diseases of the scalp to which the author has given thirty years of research, is a model of thoroughness. Dr. Sabouraud emphasizes as etiological factors, congenital syphilis, tuberculosis, and disturbances of the endocrine glands and sympathetic system. There is a bibliography of 27 pages but no index.

LABORATORY OUTLINES IN COMPARATIVE PHYSIOLOGY.
By Charles G. Rogers.
McGraw-Hill Book Co., Inc.
$1.50 $5\frac{3}{4}$ x 9; vii + 130 *New York*

ECONOMIC BENEFITS OF ERADICATING TUBERCULOSIS FROM LIVESTOCK. *U. S. Department of Agriculture Miscellaneous Publication No. 66.*
By John R. Mohler, A. E. Wight, and L. B. Ernest. *U. S. Government Printing Office*
5 cents $5\frac{3}{4}$ x $9\frac{1}{8}$; 24 (paper) *Washington*

BIOCHEMISTRY

A CHEMICAL DICTIONARY. *Containing the Words Generally Used in Chemistry, and Many of the Terms Used in the Related Sciences of Physics, Astrophysics, Mineralogy, Pharmacy, and Biology, with Their Pronunciations. Based on Recent Chemical Literature.*
By Ingo W. D. Hackh.
P. Blakiston's Son and Co., Inc.
$10.00 $6\frac{1}{2}$ x $9\frac{3}{4}$; viii + 790 *Philadelphia*

A highly useful book. The author has, with great diligence and skill, compiled a dictionary which remarkably well fulfills the requirements that such a book demands. Besides describing in simple modern terms all the terminology, theories, laws, methods, apparatus, etc., which have to do directly with chemistry, he includes the vocabulary of allied sciences and industries, and the names of investigators who have contributed to the development of chemistry. Tables, diagrams and numerous other illustrations add greatly to the value of the book.

PRAKTIKUM DER PHYSIOLOGISCHEN CHEMIE. *Zweiter Teil, Blut-Harn.* *By P. Rona and H. Kleinmann.*

Julius Springer

39.60 marks *Berlin*

5½ x 8¼; xix + 764 (paper)

This laboratory manual of the physiological chemistry of the blood and urine maintains the high standard set in the earlier parts. The present volume, which completes the work, closes with a chapter on the mathematical theory of errors, least squares, etc., by Dr. G. Ettisch. Dr. Rona, in the preface, says that he hopes that this chapter will sharpen the wits of the worker relative to the significance of the numerical results of chemical analyses. There is a detailed index.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 303.* Containing the following articles: *Methoden der Viscosimetrie kolloider Lösungen*, by Rudolf Köhler; *Methoden zur Bestimmung des kolloid-osmotischen Druckes in biologischen Flüssigkeiten*, by Marie Wreschner; *Methoden zur Bestimmung der elektrischen Struktur kolloider Stoffe, insbesondere der Biokolloide*, by Reinold Fürth.

9 marks *Urban und Schwarzenberg*

7 x 10; xx + 154 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 305.* Containing following articles: *Methodik der mitogenetischen Strahlenforschung*, by Alexander Gurwitsch; *Die Mikroveraschung*, by K. O. Henckel; *Schonendes Eindampfen bei niederen Temperaturen*, by Ernst Jantzen and Hans Schmalfuss; *Die Capillaroskopie mit starken Vergrösserungen*, by Paul Vonwiller and Alfred Vannotti; and *Der isoelektrische Punkt von Protoplasten und seine Ermittlung*, by Hans Pfeiffer.

Urban una Schwarzenberg

11 marks 7 x 10; 194 (paper) *Berlin*

Two further additions to this valuable handbook series. The first will be of great interest to the physical chemist, the latter to the experimental biologist.

A CRITICAL AND HISTORICAL STUDY OF THE PECTIC SUBSTANCES OF PLANTS. *Department of Scientific and Industrial Research, Food Investigation Special Report No. 33.*

By M. H. Branfoot.

H. M. Stationery Office

3s. 6d. net 6 x 9⅝; x + 154 (paper) *London*

This monograph deals with the chemistry of the pectic compounds, as well as their functions in the plant economy and the action of fungi and bacteria on them. The results are of value in the storage of fruits, the making of fruit jellies, and the retting of flax. There are an index of authors and a bibliography.

SEX

LAWS CONCERNING BIRTH CONTROL IN THE UNITED STATES.

Committee on Federal Legislation for Birth Control

25 cents 5⅜ x 8; 39 (paper) *New York*

This is a useful pamphlet to preserve for reference. It quotes the laws relative to birth control in each state having them. Curiously enough, there is only one state in the Union, Mississippi, which clearly prohibits a physician from giving information on the subject to his patients. Connecticut alone prohibits the *use* of contra-

ception. The laws of 26 states do not mention the prevention of conception.

WHAT IS RIGHT WITH MARRIAGE. *An Outline of Domestic Theory.* *By Robert C. Binkley and Frances W. Binkley.* *D. Appleton and Co.* $2.50 5¼ x 8; xii + 262 *New York*

Unlike most present-day books on marriage, this is a Credo rather than a case study. The authors, a young married couple trained in the social sciences, obtain their "outline of domestic theory" in large part deductively from postulates as to the nature of the family. They conclude that, while the family has been stripped of many of its former functions by other agencies, it still serves the "affectional" function and the consequent enhancement of personality. As to sex monopoly they conclude "that the ideal is good as a plan of life, but bad as an enforced element of the marriage institution."

BIOMETRY

THE DEVELOPMENT AND GROWTH OF THE EXTERNAL DIMENSIONS OF THE HUMAN BODY IN THE FETAL PERIOD. *By Richard E. Scammon and Leroy A. Calkins.* *University of Minnesota Press* $10.00 8⅜ x 11½; xxiii + 367 *Minneapolis*

The present publication is a report on a part of a systematic quantitative study of the growth and structure of the body during the fetal period. It consists of an account of the changes in the dimensions and external proportions of the body as determined from a large number of original observations and from a colligation of all available published data of other investigators. These data have been treated analytically, studied for the effects of various important artifacts upon them, and are presented in condensed tabular, graphic, and analytic forms. As a whole, the investigation has been directed to the study of the trends of central tendency of the various dimensions, although certain observations regarding their variability are included.

The most important conclusion reached is that concerning the interrelationships of the various external dimensions of the body in the fetal period. It is stated by the authors as follows:

First, the growth of the external dimensions of the body in the fetal period is directly proportional to the linear growth of the body as a whole and that of other external dimensions of the body.

Second, the absolute growth rate of each external dimension of the body, with respect to the absolute linear growth rate of the body as a whole, is usually established when the fetus is between 3 and 10 cm. in crown-heel length, and remains unchanged to birth.

The whole monograph is done with meticulous care of detail, and sound biometric reasoning applied to the general analysis. There is a complete bibliography alphabetically arranged and summaries of original data and biometric constants but unfortunately no general index. It will stand for some time as the definitive work in its field.

PHYSICAL MEASURES OF GROWTH AND NUTRITION. *School Health Research Monographs Number II.* *By Raymond Franzen.* *American Child Health Assoc.* $1.00 (paper) *New York* $1.25 (cloth) 6½ x 9½; xii + 138

This investigation was based on measurements of about 7500 public school children of the fifth and sixth grades in seventy schools scattered over 38 states. Its main object was to obtain a testing method to be used in the development of school health programs. The children

were of both sexes, white, American born, of 10, 11 and 12 years. The analysis of the anthropometrical measurements yields much interesting and valuable data in the general field of growth, development and nutrition. Much of this is presented in tabular form. At the end of chapter III is a summary of the measures which were found to yield satisfactory results in obtaining an approximation to the nutritional status of the individual. They are as follows:

> Actual weight minus the weight to be expected from height. Actual weight minus the weight to be expected from height, bisacromial width, chest dimensions, and width of hips. Actual upper arm girth minus the upper arm girth to be expected from height, chest dimensions, and width of hips. Actual calf girth minus the calf girth to be expected from height, chest dimensions, and width of hips. Actual amount of subcutaneous tissue over the biceps minus the amount of subcutaneous tissue over the biceps to be expected from height, chest dimensions, width of hips, and bisacromial width.

Appendices at the end of the report give: (a) Technique followed in obtaining physical measurements, (b) Basic data, (c) Statistical technique, and (d) Supplementary data.

PSYCHOLOGY AND BEHAVIOR

MASTER OF MY FATE. *A Discussion of Personality and Behavior with Emphasis upon Self-Direction.*
By Herschel T. Manuel. *The Century Co.*
$3.00 $5\frac{1}{8}$ x $7\frac{7}{8}$; xii + 329 *New York*

This book is so good, so terribly good, indeed so perfectly priceless, that we must confess at the start that justice cannot possibly be done to it in the limited space we can spare. Up to the present the production of those fundamentally important and valuable elements of our native fauna, the 100 per cent American, the Rotarian, and Mr. Babbitt, has been left mainly to chance and the operation of undirected natural forces. Human biology is a young science, and has not yet, up to now, done much in the way of the constructive development of a scientific technique for the mass production of a standardized, sound citizenry. Now we have a pioneer treatise, which *may*, of course, possibly be improved upon with the passage of time, but we doubt it. The author is Professor of Educational Psychology at the University of Texas. The book is obviously written *con amore*, and we recommend it with completely equal lack of reservation to all those who want to become Babbitts and to all those who don't, which makes it almost unanimous.

The book is divided into three parts. The first deals with biological and psychological foundations of human behavior. The treatment of these matters is along sound lines, but in no way so extraordinary as to warrant writing home about it. The second and major part of the book is where the really constructive and forward-looking contribution finds its home. It has to do with the development of personality and behavior along right lines. It includes chapters on such basic matters as appearance, manners, the quest of culture, character and morals, etc. A few of the section heads in this part of the book will indicate how thorough, and how right, it all is. We start with "Another reason for a bath," and go on to good advice about "Soap, water and perfume." Then come concise but adequate instructions about how to shake hands. A short, but how useful section, suggests that "Unpleasant sounds will not make friends," and points out that smacking the lips, drawing air through the teeth, noisy sipping of tea, and various other such sounds are to be avoided in building personality.

(Reginald the Office Boy says that, in the interest of that systematic thoroughness which has been instilled into him as an ideal, he thinks the Professor might well have made his list of unpleasant sounds even more inclusive than he did.)

To continue: What could be more helpful than the advice to "Stand tall and sit straight." A section of "Retouching better than masking" gives the girls superb instruction in the art of really effective make-up. Dress is thoroughly gone into; "Dress is more than drapery," "Line and form a first consideration," "Consider the silhouette," are sample sections. Then follows a priceless chapter on the general principles of effective action. We should like to quote from it, but space is lacking. There follows a chapter on language and speech, in which sections are devoted to such matters as: "Penmanship should be legible," "The voice can be improved," "The dictionary might help," "Avoid a lazy jaw," "Effective speech requires thinking." The next chapter tells of "Self and the other fellow," which instructs in friendliness. This leads naturally to "Manners in making men." Here Emily Post (whose great treatise is appropriately included in the bibliography) finds a rival, and a dangerous one. What could be more perfect than this section headed "Chew your gum in private," which we must quote in full:

> Unnecessary practices should be avoided where they are likely to annoy others. The chewing of gum, the eating of candy and the use of tobacco are frequent transgressions of this principle. Nor can one justify the lack of privacy too frequently shown in powdering the nose, manicuring the nails and combing the hair. It is not universally entertaining to have thrust before one the monotonous grind of a lower jaw, the nervous sucking at a cigarette or the dab-dab-dab of an attempt to restore a vanishing complexion.

Detailed instructions are given about introducing people to each other, how to behave at the table—no "thoughtful reader," to whom the publisher's blurb recommends the book, need ever again be embarrassed about toothpicks, forks, soup, etc.—getting up a dance, and so on, and so on. Paragraph No. 15 of the table instructions contains the following sentence, which illustrates the soundness and candor of the whole: "Alcoholic drinks or other harmful articles should be courteously declined."

Here we must regretfully leave Part II. There is a lot more of it, but if what we have already called attention to does not make the reader of this review dash out and buy the book at once, our hand has wholly lost its cunning.

Part III presents a program of self-direction, and is largely composed of a "rating scale." This "rating scale" contains 502 separate items. You are instructed to rate yourself 0, 1, or 2 relative to each of these items. The meaning is that 0 is the least desirable rating, 2, the most desirable rating, and 1 average. By the use of this scale according to directions "the ambitious individual may analyze his difficulties and initiate efforts toward improvement."

We can bring to a close this all too brief notice of a great book in no more fitting manner than by quoting that sublime thought of Samuel Butler:

Oh God! Oh Montreal!

BRAIN MECHANISMS AND INTELLIGENCE: *A Quantitative Study of Injuries to the Brain.*
By K. S. Lashley.
The University of Chicago Press *Chicago*
$3.00
6 x 9; xiv + 186 + 11 plates

The investigation herein reported is part of a general program on the analysis of the neural mechanisms which play a part in learning. Dr. Lashley has done a re-

markably fine piece of work, and his results are of the utmost importance in the field of neurological investigation. He has adequately summarized his study on the last two pages of his book. Unfortunately space will permit in this review only the inclusion of the inferences which he draws from his experiments:

> The learning process and the retention of habits are not dependent upon any finely localized structural changes within the cerebral cortex. The results are incompatible with theories of learning by changes in synaptic structure, or with any theories which assume that particular neural integrations are dependent upon definite anatomical paths specialized for them. Integration cannot be expressed in terms of connections between specific neurons.
>
> The contribution of the different parts of a specialized area or of the whole cortex, in the case of nonlocalized functions, is qualitatively the same. There is not a summation of diverse functions, but a nonspecialized dynamic function of the tissue as a whole.
>
> Analysis of the maze habit indicates that its formation involves processes which are characteristic of intelligent behavior. Hence the results for the rat are generalized for cerebral function in intelligence. Data on dementia in man are suggestive of conditions similar to those found after cerebral injury in the rat.
>
> The mechanisms of integration are to be sought in the dynamic relations among the parts of the nervous system rather than in details of structural differentiation. Suggestions toward a theory of the nature of these forces are presented.

The author devotes a chapter to the comparison of his experiments on rats with experiments on the dog, the monkey, and man. The book is illustrated with numerous figures showing the brain lesions of the animals under experimentation, and with tables exhibiting the performance of these animals.

There is a bibliography of 137 titles, and an index.

EXPERIMENTAL STUDIES OF ADAPTIVE BEHAVIOR IN CATS. *Comparative Psychology Monographs, Vol. 6, No. 1.*
By Donald K. Adams.
The Johns Hopkins Press
$2.50 7 x 10¼; 168 (paper) *Baltimore*

The author comes out strongly against the description of psychology in terms of the conditioned reflex of the behaviorist. He maintained a colony of cats in the Yale Institute of Psychology for three years, and performed experiments upon them in three of the Thorndike puzzle boxes. "In each case the presence of what Hobhouse calls practical ideas is inferred. The presence of articulate ideas is inferred from the behavior of Pete in box A, from that of Trey in Box Bl and from that of Fitz in Box C and is suggested by other behavior." He reaches a theory that agrees with that stated by Tolman in 1928, a summary of which is quoted in the text.

GROWTH IN RELIGION. *An Introduction to Psychology for Teachers of Religion.*
By Harold J. Sheridan. *Cokesbury Press*
$1.00 4⅞ x 7¼; 192 *Nashville, Tenn.*

This interesting book is supposed to be a text for the training of teachers of religion. Its strategy seems to be extremely subtle. There is nothing like a frontal attack on the problem—indeed the book seems almost oriental in its directness. It discusses such matters as endocrine glands, growth, variation of man in stature, and so on. There is an obvious striving throughout towards a scientific viewpoint and attitude of mind. The book is moderate in tone on religious matters throughout.

DEVELOPED LESSONS IN PSYCHOLOGY. *Including Tests with Norms.*
By H. Meltzer and E. M. Bailor.
Harcourt, Brace and Co.
$1.50 5 x 7¾; x + 199 *New York*

The authors have had the brilliant idea of applying some of the pedagogical principles developed in the study of educational psychology to the teaching of psychology itself.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

QU'EST-CE QUE LA MÉDECINE? *suivi de Six Autres Essais.*
By E. Rist. *Masson et Cie*
25 francs 5½ x 9; 236 (paper) *Paris*

These seven essays, so brilliant, so judicious, so intelligent, by a great living master, make a notable contribution to the *belles lettres* of medicine. The titles are: "What is medicine?"; "The diagnosis of diseases of the chest before the invention of percussion and auscultation;" "The beginnings of percussion;" "The progress of medicine;" "Science and art in medicine;" "Some moral responsibilities of the physician;" "The Hippocratic oath." In spite of the apparent diversity of these topics there runs through the whole a unifying red thread. Dr. Rist essays, in these pages, an *apologia* for medicine and physicians. He says truly that medicine and physicians have often been sharply and penetratingly criticised, and he wishes to present the other side of the case. He thinks that he is likely to be exonerated of any charge of being a biassed witness because he himself is a physician, on the ground that his defense of medicine and its practitioners will perhaps be relished least of all by physicians themselves.

This book should be translated into English. Surely enterprising American publishers will not miss such an opportunity.

SCIENCE AND THE UNSEEN WORLD.
By Arthur S. Eddington. *The Macmillan Co.*
$1.25 4½ x 8; 91 *New York*

As in the latter chapters of his "Nature of the Physical World" noted in these columns in a previous issue, the author expands his thesis that science is not enough. There is a realm of experience that can not be comprehended in the symbols of science.

> There is an hour of the Indian night, a little before the first glimmer of dawn, when the stars are unbelievably clear and close above, shining with a radiance beyong our belief in this foggy land. The trees stand silent around one with a friendly presence. As yet there is no sound from awakening birds; but the whole world seems to be intent, alive, listening, eager. At such a moment the veil between the things that are seen and the things that are unseen becomes so thin as to interpose scarcely any barrier at all between the eternal beauty and truth and the soul which would comprehend them.

Science can not deny the reality of this clearly felt, unseen world; science has ceased to identify the real and the concrete even in its own domain of physics. In this unseen world, religion and God somehow have play, but Eddington is a Quaker and does not advocate any credal doctrine of what God is or how he works.

As a statement of the religious faith of a great contemporary scientist, the book has some significance, but hardly so as a contribution to religious or metaphysical philosophy. Religion has no special sanction over any profane aestheticism so far as is revealed here, and the logic of the author's reasoning is frequently dubious.

PROCESS AND REALITY. *An Essay in Cosmology. Gifford Lectures Delivered in the University of Edinburgh During the Session 1927–28.*
By Alfred N. Whitehead.
The Macmillan Co.
$4.50 5¾ x 8½; xii + 545 *New York*

In these Gifford Lectures Professor Whitehead has developed and extended his organism philosophy. Further he has matured it. So far as his readers are concerned his views on organism as a fundamental philosophical point of departure were presented in what may perhaps fairly be called an adolescent condition in *Science and the Modern World*. In the present book they are as if grown up, and certainly they are made to do a man's work. For here Whitehead does what he says all truly constructive philosophy must do; namely, having set up a system of ideas, it must "unflinchingly . . . explore the interpretation of experience in terms of that scheme." *Process and Reality* is no minor effort. It is an attempt to enquire into the nature of things on a cosmical scale of comprehensiveness. The book is difficult, but it will be profitable reading for the biologist.

THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. *A Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, etc., with the Pronunciation, Derivation, and Definition.*
By W. A. Newman Dorland.
W. B. Saunders Co.
Philadelphia
$7.00 net, flexible binding, plain
$7.50 net, flexible binding, thumb index
6 x 9; 1427